THE UNIVERSITY OF QUEENSLAND

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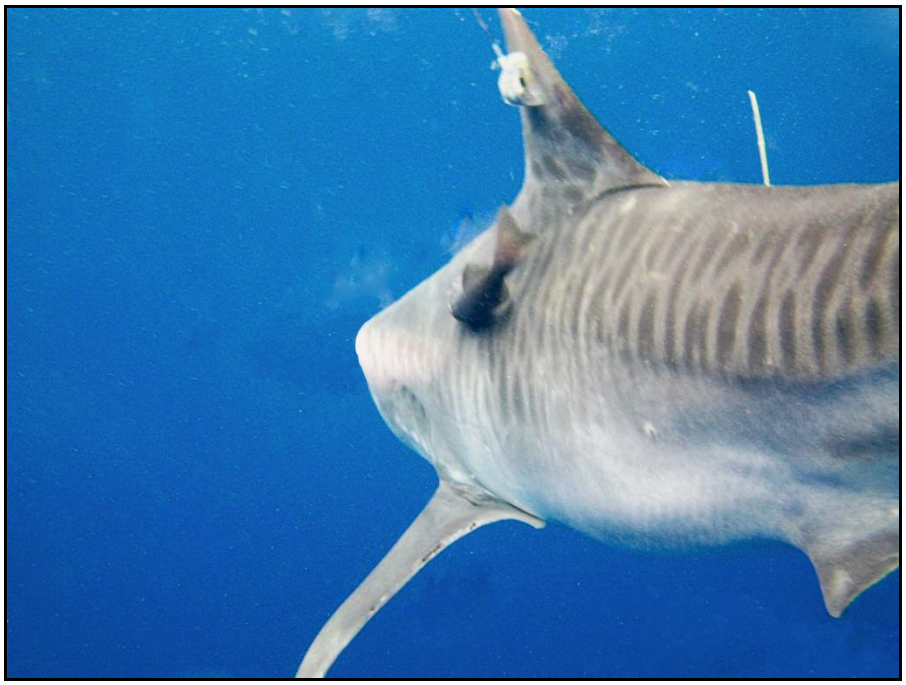
The biology and ecology of the tiger shark (*Galeocerdo cuvier*) on the east coast of Australia.

Bonnie Jane Holmes

BSc (Hons)



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ABSTRACT

The tiger shark (*Galeocerdo cuvier*) (Péron and Lesueur 1822) is the largest of the carcharhinids, with a circumglobal distribution in both tropical and warm temperate coastal and pelagic waters. In the western Pacific, *G. cuvier* movements are wide-ranging, encompassing the east coast of Australia and south Pacific Islands. Throughout the region, *G. cuvier* is exposed to a range of commercial, recreational, artisanal and illegal foreign fishery impacts, as both a target and by-product species. Listed as 'near threatened' on the International Union for Conservation of Nature (IUCN) Red List, suitable long term species-specific catch, catch rate and biological data are seldom available for large shark species like *G. cuvier*, particularly where historical commercial fishery logbook reporting has been poor.

Shark control programs targeting large sharks along Australia's east coast have been in operation for over 60 years, using relatively standardised fishing gear in nearshore waters all year round, with historical catch and effort data recorded by shark contractors. Historical catch, catch rate and biological data collected through the Queensland Shark Control Program (QSCP) since 1993 were investigated, which revealed significant declines ($p < 0.05$) in catch rates of *G. cuvier* at some tropical and all sub-tropical locations along the Queensland coast. Significant temporal declines in the average size of *G. cuvier* also occurred at four of the nine locations analysed ($p < 0.05$), which could be indicative of fishing reducing abundance in these areas. Inter-annual variability in catches at each location was considerable and warranted careful interpretation with respect to estimating population abundance from these data. Investigation into the spatial and temporal movements of tiger sharks, and how their abundances fluctuate in relation to environmental influences, provided a basis for determining the factors driving this variability.

Tiger shark movements were recorded using PAT Mk-10 and SPOT5 electronic tags to investigate *G. cuvier* spatial dynamics, site fidelity and habitat use off the east coast of Australia. Of the 18 tags deployed, 15 recorded information on depth and/or temperature, and horizontal movements, with tracking times ranging between four and 408 days. Horizontal movements were characterised by combinations of resident and transient behaviour that coincided with seasonal changes in water temperature, with summer migrations from sub-tropical Queensland waters to the southern temperate

waters of New South Wales (NSW) to exploit the seasonally warm and prey abundant waters. While the majority of movement activity was focused around the continental slope, large-scale migration was evident with one individual moving from offshore Sydney, Australia, to New Caledonia (≈ 1800 km) in 48 days. Periods of tiger shark residency outside of Australia's fisheries management zones highlighted the potential vulnerability of the species to unregulated fisheries, and the importance of cross-jurisdictional arrangements for migratory species' management and conservation.

Understanding the life history strategies of commercially- and recreationally-exploited elasmobranchs is fundamental in implementing appropriate fisheries management regimes. Lengths-at-age and growth rates for *G. cuvier* captured on the east coast of Australia were estimated from vertebral growth band counts of 202 sagitally-sectioned centra from 112 females (71 – 430 cm total length (TL)) and 79 males (72 – 351 cm TL). Modelled growth coefficients for pre- and post-natal females (L_∞ = 418.3, L_0 = 101.5, k = 0.07) and males (L_∞ = 350.5, L_0 = 101.6, k = 0.12) were smaller than those previously reported for tiger shark populations in other regions of the world. The population sampled herein included older tiger sharks than previously aged elsewhere, with split-band and narrow banding patterns in large individuals being identified as potential sources of age underestimation.

G. cuvier is the only carcharhinid with an aplacental viviparous reproductive mode. Its large size and semi-solitary nature has made the species' reproductive parameters difficult to study, particularly for mature animals that exceed 300 cm total length (TL). I present the first analysis of the reproductive biology of *G. cuvier* from data and specimens obtained from the QSCP and from NSW game fishing tournaments. Pups (n = 112) from four pregnant sharks were used to assess the possibility of multiple paternity. Length at 50% maturity (L_{50}) was 297 cm TL for males and 325 cm TL for females. Historical QSCP data for 83 litters indicate that parturition occurs when pups are 70 – 90 cm TL, and that considerable variation in pup size from the same litter does occur. Birth is in the austral summer after a gestation period of around 15 – 16 months. Female sharks that were pregnant, or had well-developed oocytes, or had small oocytes were found throughout the year, consistent with a triennial breeding cycle. There was no evidence of multiple paternity, based on the litters of the four sharks examined using nine microsatellite loci, which may have implications for the genetic diversity of this population.

DECLARATION BY AUTHOR

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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PUBLICATIONS DURING CANDIDATURE

PEER-REVIEWED PAPERS

Holmes, B.J., Peddemors, V.M., Gutteridge, A. N., Geraghty, P.T., Chan, R.W.K., Tibbetts, I.R. and Bennett, M.B. (In Press). Age and growth of the tiger shark (*Galeocerdo cuvier*) on the east coast of Australia. *Journal of Fish Biology.*

Holmes, B.J., Pepperell, J.G., Griffiths, S.P., Jaine, F.R.A., Tibbetts, I.R. and Bennett, M.B. (2014). Tiger shark (*Galeocerdo cuvier*) movement patterns and habitat use determined by satellite tagging in eastern Australian waters. *Marine Biology* **161**(11): 2645–2658.

Holmes, B.J., Sumpton, W.D., Mayer, D.G., Tibbetts, I.R., Neil, D.T. and Bennett, M.B. (2012). Declining trends in annual catch rates of the tiger shark (*Galeocerdo cuvier*) in Queensland, Australia. *Fisheries Research* **129-130**: 38–45.

Dudgeon, C.L., Blower, D.C., Broderick, D., Giles, J.L., **Holmes, B.J.**, Kashiwagi, T., Kruck, N.C., Morgan, J.A.T., Tillett, B.J. and Ovenden, J.R. (2012). A review of the application of molecular genetics for fisheries management and conservation of shark and rays. *Journal of Fish Biology* **80**: 1789–1843.

Holmes, B.J. and Neil, D.T. (2012). "Gift Giving" by wild bottlenose dolphin (*Tursiops sp*.) to humans at a wild dolphin provisioning program, Tangalooma, Australia. *Anthrozoös* **26**(4): 397–413.

CONFERENCE ABSTRACTS

Oral presentations

Bonnie J. Holmes, Wayne D. Sumpton, David G. Mayer, David T. Neil, Mike B. Bennett and Ian R. Tibbetts. Evidence of significant declines in tiger shark (*Galeocerdo cuvier*) catch rates based on historical Queensland Shark Control Program data, with notes on reproductive parameters. Sharks International Conference, June 2010, Cairns, Queensland.

Bonnie J. Holmes, Wayne D. Sumpton, David G. Mayer, David T. Neil, Mike B. Bennett and Ian R. Tibbetts. Declining trends in annual catch rates of the tiger shark (*Galeocerdo cuvier*) in Queensland, Australia. The University of Perpignan Via Domitia, Invited Speaker, September 2012, Perpignan, France.

Bonnie J. Holmes, Julian G. Pepperell, Shane P. Griffiths, Fabrice R.A. Jaine, Ian R. Tibbetts and Mike B. Bennett. Tiger shark (*Galeocerdo cuvier*) movement patterns and habitat use determined by satellite tagging in eastern Australian waters. Oceania Chondrichthyan Society, Annual Conference, September 2013, Brisbane, Queensland.

Bonnie J. Holmes, Julian G. Pepperell, Shane P. Griffiths, Fabrice R.A. Jaine, Ian R. Tibbetts and Mike B. Bennett. Do tiger sharks (*Galeocerdo cuvier*) undertake partial migrations at high latitudinal locations? Movement and habitat use on the east coast of Australia. Sharks International Conference, June 2014, Durban, South Africa.

Poster presentations

Bonnie J. Holmes and Wayne D. Sumpton. Preliminary results on the biology and distribution of tiger shark (*Galeocerdo cuvier*) in Queensland based on data from the Shark Control Program. Oceania Chondrichthyan Society, Annual Conference, September 2008, Sydney, New South Wales.

Bonnie J. Holmes, Julian G. Pepperell, Shane P. Griffiths, Mike B. Bennett, Jenny R. Ovenden, David T. Neil and Ian R. Tibbetts. Tiger shark (*Galeocerdo cuvier*) habitat use and movement patterns in south eastern Australian waters. Oceania Chondrichthyan Society, Annual Conference, September 2011, Gold Coast, Queensland.

Bonnie J. Holmes, Julian G. Pepperell, Shane P. Griffiths, Fabrice R.A. Jaine, Ian R. Tibbetts and Mike B. Bennett. Long-term movement patterns of satellite tagged tiger sharks (*Galeocerdo cuvier*) in south eastern Australia. American Elasmobranch Society, Annual Conference, August 2012, Vancouver, Canada.

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CHAPTER 2

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Contributor	Statement of contribution
Holmes, B.J. (Candidate)	Designed experiments (70%) Analysed the data (70%) Wrote the paper (80%)
Sumpton, W.D.	Designed experiments (30%) Analysed the data (10%) Wrote and edited paper (10%)
Mayer, D.G.	Analysed the data (20%) Wrote and edited paper (4%)
Tibbetts, I.R.	Wrote and edited paper (2%)
Neil, D.T.	Wrote and edited paper (2%)
Bennett, M.B.	Wrote and edited paper (2%)

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Holmes, B.J. (Candidate)	Designed experiments (70%) Analysed the data (70%) Wrote the paper (85%)
Pepperell, J.G.	Designed experiments (30%)

	Wrote and edited paper (5%)
Griffiths, S.P.	Analysed the data (28%) Wrote and edited paper (4%)
Jaine, F.R.A.	Analysed the data (2%) Wrote and edited paper (2%)
Tibbetts, I.R.	Wrote and edited paper (2%)
Bennett, M.B.	Wrote and edited paper (2%)

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Holmes, B.J. (Candidate)	Designed experiments (90%) Collected data (80%) Analysed the data (73%) Wrote the paper (85%)
Peddemors, V.M.	Designed experiments (10%) Analysed the data (20%) Wrote and edited paper (5%)
Gutteridge, A.N.	Analysed the data (5%) Wrote and edited paper (2%)
Geraghty, P.T.	Analysed the data (2%) Wrote and edited paper (2%)
Chan, R.W.K.	Collected data (20%) Wrote and edited paper (1%)
Tibbetts, I.R.	Wrote and edited paper (2%)
Bennett, M.B.	Wrote and edited paper (3%)

CONTRIBUTIONS BY OTHERS TO THE THESIS

CHAPTER 1

The introduction is my own work. My supervisors, I.R. Tibbetts, M.B. Bennett, J.R. Ovenden and D.T. Neil assisted with editorial changes to earlier versions of the chapter.

CHAPTER 2

This chapter was published in *Fisheries Research* in June 2012. I am the senior author and W.D. Sumpton, D.G. Mayer, I.R. Tibbetts, D.T. Neil and M.B. Bennett are co-authors. W.D. Sumpton provided the data from the Queensland Shark Control Program and assisted with data analysis. D.G. Mayer assisted with the model development and statistical analysis. N. Engstrom and T. Zahmel provided maps and commercial fishing data from Fisheries Queensland. A. Gutteridge, S. Taylor and K. Townsend provided comments on earlier versions of the manuscript. All co-authors assisted with progress and final manuscript editing.

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This chapter was accepted for publication in *Journal of Fish Biology* in March 2015. I am the primary author and V.M. Peddemors, A.N. Gutteridge, P.T. Geraghty, R.W.K. Chan, I.R. Tibbetts and M.B. Bennett are co-authors. V.M. Peddemors was

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STATEMENT OF PARTS OF THE THESIS SUBMITTED TO QUALIFY FOR THE AWARD OF ANOTHER DEGREE

None.

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For my daughter Addison, who was born in the middle of all of this madness – thank you baby girl for always reminding me what the more important things in life are. You are the joy and love of my life.

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KEYWORDS

Galeocerdo cuvier, tiger shark, shark control, shark fisheries, satellite tracking, migration, life history, age and growth, reproduction.

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PHOTOS

Cover photo: 'Emma' tagged off Shellharbour, NSW. Photo: G. Barea.

Chapter 1: 'Sydney' tagged off Fraser Island, QLD. Photo: R. Snow, Ocearch.

Chapter 2: Tiger shark drumline catch, Sunshine Coast, QLD. Photo: P. Dimond, Queensland Shark Control Program.

Chapter 3: 'Shania' tagged off Port Hacking, NSW. Photo: G. Barea.

Chapter 4: Sectioned vertebrae. Photo: B. Holmes.

Chapter 5: Tiger shark pups. Photo: B. Holmes.

Chapter 6: Captured shark. Photo: B. Holmes.

DEDICATION

For my family….

….and for the sharks…..

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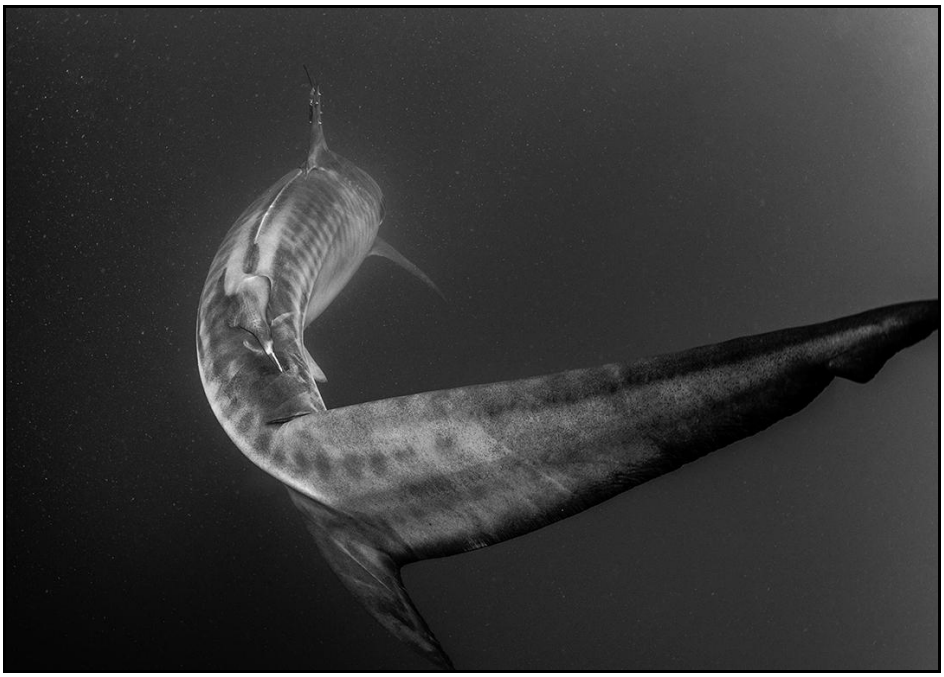
ABBREVIATIONS

A_{50}	Age at 50% Maturity
AIC	Akaike's Information Criterion
ANOVA	Analysis of Variance
APE	Average Percentage Error
CGLM	Conditional Generalised Linear Model
CI	Confidence Intervals
CPUE	Catch per Unit Effort
CV	Coefficient of Variation
dNTP	Nucleoside Triphosphate
DMSO	Dimethyl Sulfoxide
DNA	Deoxyribonucleic Acid
EAC	East Australian Current
EEZ	Exclusive Economic Zones
FFT	Fast Fourier Transform
FL or L_F	Fork Length
GOM3	3-Parameter Gompertz Model
HWE	Hardy Weinberg Equilibrium
IUCN	International Union for the Conservation of Nature
KZN	KwaZulu-Natal
L_{50}	Length at 50% Maturity
LC	Location Class
LOGI3	3-Parameter Logistic Model
M	Mass
MIR	Marginal Increment Ratio
MMI	Multi-model Inference
MOD	Maximum Oocyte Diameter
MW	Margin Width
NSW	New South Wales
NSWSMP	New South Wales Shark Meshing Program
NSWFOP	New South Wales Fisheries Observer Program
PA	Percentage Agreement
PAT	Pop-Up Archival Tag
PBW	Previous Band-Pair Width
PCL or L_{PC}	Precaudal Length
PCR	Polymerase Chain Reaction
PIDsib	Probability of Identity of Siblings
QLD	Queensland
QSCP	Queensland Shark Control Program
ROM	Rate of Movement
SD	Standard Deviation
SPOT5	Smart Position and Temperature Transmitting Tag
SST	Sea Surface Temperature
TL or L_T	Total Length
UKF	Unscented Kalman Filter
VBGF	von Bertalanffy Growth Function
VB3	3-Parameter von Bertalanffy Model
WC-GPE	Wildlife Computers Global Position Estimator
WC-AMP	Wildlife Computers Argos Message Processor
YOY	Young-of-the-year

Chapter 1: General Introduction



1.1 CHONDRICHTHYAN FISHES

Sharks belong to the taxonomic class Chondrichthyes, or cartilaginous fishes, that emerged during the late Silurian period around 400 million years ago. Since the introduction of the Linnaean system for classifying biological organisms, about 1185 chondrichthyan species have been formally described (White and Last, 2012). There are two subclasses of chondrichthyan fishes: the Holocephali (chimaeras); and the Elasmobranchii (sharks, skates and rays), which is further divided into the Selachii (sharks) and the Batoidea (rays) (Compagno, 1990). The Selachii consists of eight orders: Pristiophoriformes (sawsharks), Squatiniformes (angelsharks), Squaliformes (dogfish sharks), Hexanchiformes (sixgilled sharks), Lamniformes (mackerel sharks), Carcharhiniformes (ground sharks), Orectolobiformes (carpetsharks), and Heterodontiformes (bullhead sharks) (Compagno et al., 2005). The Carcharhiniformes comprising of eight families constitute around 56% of all shark species (Compagno, 1990).

Requiem or whaler sharks (family Carcharhinidae) are members of the order Carcharhiniformes, with 31 of the 44 described carcharhinid species found in Australian waters (Last and Stevens, 2009). Carcharhinids inhabit offshore pelagic waters beyond the continental shelf, as well as coastal marine and inland freshwater rivers and lakes (Grace, 2001). The family contains more species considered dangerous to humans than any other, with tiger shark (*Galeocerdo cuvier*) and bull shark (*Carcharhinus leucas*) the main target species for long-term shark control programs in South Africa, Hawaii, and on the east coast of Australia (Cliff and Dudley, 1991; Reid and Krogh, 1992; Simpfendorfer, 1992a; Krogh, 1994; Last and Stevens, 1994; Dudley, 1997; Green et al., 2009; Fisheries, 2006; Reid et al., 2011). In addition, the white shark (*Carcharodon carcharias*), from the order Lamniformes, is considered a threat to humans and is also a target species in these programs. Not limited to anti-shark measures, these large elasmobranchs are targeted in a range of fisheries around the world, and complementary species-specific biological information in many regions remains scant.

1.2 LIFE HISTORY TRAITS OF ELASMOBRANCHS

Shark and ray life history strategies are typically characterised as having slow growth, late maturity and low fecundity (Holden, 1974; Hoenig and Gruber, 1990; Pratt and Casey, 1990; Last and Stevens, 2009). Holden (1977) characterised the life history traits of sharks by the 'r-K selection theory', a theoretical framework for comparing the trade-off between quantity and quality of offspring. Most teleosts are referred to as 'r' strategists, that is, they have a relatively short lifecycle characterised by fast growth and the production of numerous offspring with no maternal investment beyond the nutrients supplied in the ovum (Hoenig and Gruber, 1990). While these 'r' strategists may be able to withstand considerable levels of exploitation, they are generally less able to cope with environmental changes (Pratt and Casey, 1990; Cortés, 2004). Conversely, 'K' selected life history strategists, such as sharks, employ traits associated with living at densities close to carrying capacity, and are characteristically larger in size, have longer life expectancies, and produce fewer offspring. These traits generally render them more able to accommodate environmental change (Chin et al., 2010), but limit their ability to withstand the additional mortality resulting from fisheries exploitation (Holden, 1974; Pratt and Casey, 1990). Consequently, sustainable management of shark harvest is often difficult, particularly when there is little biological information available to assess a population's vulnerability to fishing.

Unlike the broadcast spawning and external fertilization of many teleost species, all elasmobranchs undergo internal fertilisation. While a few shark families still employ an egg-laying oviparous reproductive strategy, the majority are viviparous, forming a placental attachment to the mother. All carcharhinids use a viviparous, placental reproductive mode with the exception of *G. cuvier*, which is the only carcharhinid that uses aplacental viviparity. This reproductive mode allows the pups to develop for longer before being born, meaning that they can achieve larger sizes at birth. Carcharhinid size-at-maturity, gestation period, litter size and breeding periodicity has been found to vary considerably among species. Nevertheless, all carcharhinids produce relatively well-developed young that are less prone to predation and environmental stress than the early life stages of teleosts (Wourms and Demski, 1993; Hoenig and Gruber, 1990; Carrier et al., 2004; Last and Stevens, 2009). However, investment in the production of well-developed young comes at a high

energetic cost, often resulting in lower fecundity than that achieved by an ‘r’ strategist.

It is common for female carcharhinids to mature later, and at a larger size than males (Branstetter et al., 1987; Wintner and Cliff, 1996; Driggers et al., 2004). Viviparity restricts fecundity, and there is a direct relationship between the size of the mother and the size and/or number of the young produced (Branstetter, 1981). The relationship between the length of the mother and litter size may be variable before maximum adult size is reached in some species, such as the sandbar shark (*Carcharhinus plumbeus*) and spinner shark (*Carcharhinus brevipinna*) (Joung and Chen 1995; Capape et al. 2003), but has been found to be linear in others, such as the spot tail shark (*Carcharhinus sorrah*) and black tip shark (*Carcharhinus tilstoni*) (Harry et al. 2013). Smaller carcharhinid species generally breed annually (Simpfendorfer, 1992b), while most other carcharhinids breed biennially (Branstetter, 1981). Two of the largest carcharhinids, the dusky shark (*Carcharhinus obscurus*) and *G. cuvier* are believed to breed triennially (Clarke and von Schmidt, 1965; Whitney and Crow, 2007). Coupled with their slow growth and late maturation, carcharhinids that do not reproduce every year may be susceptible to overexploitation (Stevens et al., 2000).

Understanding rates of growth is an important component of shark life-history studies, particularly for juveniles. The attainment of a size large enough to deter predation by larger sharks appears to be an integral constraint on the recruitment of neonates and juveniles to the adult population (Branstetter, 1990; Heupel and Simpfendorfer, 2011; Guttridge et al., 2012). Some species, such as the Australian sharpnose shark (*Rhizoprionodon taylori*), rely on fast growth rates (Simpfendorfer, 1999) while other species, such as *G. cuvier*, will occupy different habitats to their larger counterparts to avoid predation (Lowe et al., 1996). Some species, such as the blacktip shark (*Carcharhinus limbatus*), rely on the use of nursery areas in part due to the greater protection provided by the increased number of conspecifics (Castro, 1996; Heupel and Simpfendorfer, 2002). Some carcharhinids, such as *C. leucas*, produce relatively few, but large offspring that may exhibit slow growth as they are less prone to predation during their juvenile, freshwater/estuarine habitat occupancy phase (Branstetter and Stiles, 1987).

Age and growth rate also varies considerably among the carcharhinids. Maximum body size ranges from about 80 cm total length (TL) in *R. taylori* (Simpfendorfer, 1993; Taylor and Bennett, 2013), to around 550 cm in *G. cuvier* (Meyer et al., 2014). To date, reported maximum ages of carcharhinids range from 4+ years in the blacknose shark (*Carcharhinus acronotus*) (Carlson et al., 1999), up to 33+ years in *C. obscurus* (Natanson et al., 1995; Simpfendorfer et al., 2002; Geraghty et al., 2014). Species may also differ considerably between locations in terms of growth rate (Tanaka et al., 1990; Lessa et al., 2004; Harry et al., 2013; Gutteridge et al., 2013; Meyer et al., 2014), longevity (Wintner and Dudley, 2000; Allen and Wintner, 2002; Geraghty et al., 2014), size-at-maturity (Parsons, 1993; Frisk et al., 2001; Francis and Duffy, 2005; Semba et al., 2011; Montealegre-Quijano et al., 2014) and maximum size (Pratt and Casey, 1990; Cortés, 2000; Allen and Wintner, 2002; Carlson and Baremore, 2005; Neer et al., 2005; Meyer et al., 2014), which suggests that age and growth assessments may be of value in the understanding of individual populations of target species.

1.3 MOVEMENT ECOLOGY

'Movement ecology' refers to the quantitative study of various aspects of the movements of living organisms. A burgeoning field of research, movement ecologists attempt to predict when and where an animal may choose to move based on observing an organism's conditional strategies, which are based on fixed intrinsic states (e.g. age and sex) as well as flexible extrinsic states (i.e. prey abundance and temperature) to determine habitat use (Papastamatiou et al., 2013). With recent advances in tagging technology, our capacity to follow the individual movements of animals has led to a greater understanding of the behaviours, movements, and physiology of a given species (Brill et al., 1993; Kohler and Turner, 2001; Cooke et al., 2004; Ropert-Coudert et al., 2010; Sims et al., 2011), which is of particular importance in aquatic environments where traditional methods of animal tracking cannot be realised. Remote monitoring of geographical position, swimming depth and water temperature allows researchers to make inferences about how aquatic predators utilise their surrounding environment, providing insights into their behavioural ecology (e.g. see Holland et al., 1999; Bonfil et al., 2005; Domeier, 2006; Carlson et al., 2010; Barnett et al., 2011; Block et al., 2011; Bunnefeld et al., 2011). Accessing these types of data,

particularly for large apex predators that have the ability to influence the structure and function of marine communities, are essential for the development of future population models and implementation of region-specific conservation initiatives (Heithaus et al., 2008).

Migration is a specific type of movement that may be persistent or seasonal, often featuring highly-directional, long distance travel (Alerstam et al., 2003; Dingle and Drake, 2007). Acting at multiple scales, animal migration may influence population structure, govern ecosystem dynamics, and influence evolutionary processes and patterns of local and global biodiversity (Nathan et al., 2008). However, in most animal populations only a proportion of the population migrates, that is, individuals display either resident or migrant behaviour – a process known as partial migration (Skov et al., 2010; Broderson et al., 2011; Chapman et al., 2011). In a growing number of examples, individuals within populations show differences in migratory behaviour, with some individuals migrating between habitats while others remain resident in a single habitat (Dingle, 1996). As a result, both the timing of migration, and the resident/migratory fraction in partially migrating populations are likely to vary between years and populations (Cagnacci et al., 2011; Mysteraud, 2011; Broderson et al., 2011). Within aquatic communities, recent studies suggest that all groups of fishes demonstrate partial migration, including oceanodromous top predators such as sharks (Chapman et al., 2012; Papastamatiou et al., 2013). Indeed the partial migration of predatory elasmobranchs, whose movement patterns may be shaped by the dynamics of the surrounding environment, will have consequences for ecological processes, and may influence fisheries management and conservation strategies (Forchhammer et al., 2002; Papastamatiou et al., 2013). A greater understanding of the spatio-temporal movements of marine predators is of particular importance when assessing population-level changes in abundance, and when analysing historical catch rate information.

1.4 FISHERY IMPACTS: COMMERCIAL AND RECREATIONAL FISHERIES

The importance of large sharks as apex predators in marine ecosystems has been widely documented (Stevens et al., 2000; Myers et al., 2007; Heithaus et al., 2008, Ferretti et al. 2010; Dulvy et al., 2013). However, it is those large, slow-growing, late-maturing sharks (which include most carcharhinids and sphyrnids) that are the least

resilient to fishing mortality (Smith et al., 1998). The global decline in shark populations due to overfishing has been documented extensively, with actual mortality estimated to be as much as three times higher than documented mortality due to illegal fishing, under-reporting and unregulated fishing (Camhi et al., 1998; Baum et al., 2003; Myers et al., 2007; Lam and Sadovy de Mitcheson, 2011; Dulvy et al., 2013). Differential vulnerability to fishing pressure exists among shark species, and even among shark populations as the scale of commercial, recreational, artisanal and illegal fishing practices differs greatly among oceanic regions. Generally, large sharks are more vulnerable to exploitation as they exhibit some of the longest gestation periods and highest levels of maternal investment in the animal kingdom (Cortés, 1998; Stevens et al., 2000; Dulvy et al., 2013). Conversely, smaller, more fecund species like the gummy shark (*Mustelus antarcticus*) may be sustainably harvested (Pribac et al., 2005). Shark fisheries in the northwest Atlantic have reported population collapses of large, slow growing species, such as the sand tiger (*Odontaspis taurus*), and the dusky shark (*C. obscurus*), which show little sign of recovery. Notwithstanding, in the same fishery, more fecund and faster growing species such as the sandbar shark (*C. plumbeus*) have enabled the fishery to continue despite also showing signs of population reduction (Musick et al., 1993; Musick, 1999). Such examples illustrate the need for species-specific shark data collection and assessment for effective fisheries and conservation management.

Quantifying the impacts of fishing on large, migratory shark species is often hampered by a lack of fishing regulation and reporting in international waters, coupled with the different management and monitoring regimes of neighbouring jurisdictions (Dulvy et al., 2008). This has resulted in an increased level of threat and often an incomplete understanding of population trends for these wide-ranging species. While the more recent implementation of Marine Protected Areas (MPAs) has been successful in reducing shark population declines in some areas (Dulvy et al., 2006; Bond et al., 2012; da Silva et al., 2013), these areas seldom encompass the full home range of large migratory sharks (Knip et al., 2012). The southwest Pacific Ocean, comprising the east coast of Australia, New Zealand, and many South Pacific Islands, encompasses a complex of Exclusive Economic Zones (EEZ), territorial seas and archipelagic waters interspersed with international high seas. Recent studies on the movements of *C. carcharias* and *G. cuvier* throughout this region has shown that both species move extensively throughout these zones (Bruce et al., 2006; Werry et

al., 2014), highlighting the importance of understanding the movement ecology in a given population.

1.5 FISHERY IMPACTS: SHARK CONTROL PROGRAMS

Shark control programs are considered effective because they reduce local populations of large, potentially dangerous shark species that move into nearshore coastal waters which humans frequent (Springer and Gilbert, 1963). Fear of shark attacks, coupled with the economic considerations of regional beachside tourism, provides the justification for implementation of such programs usually managed by local governments. Long-term catch and catch rate trends for large sharks are difficult to obtain, and commercial logbook information has long been compromised by limited species-level reporting and inaccurate fishing effort information (Punt et al., 2000; Clarke et al., 2006). The use of shark control program information for deriving catch rate trends is advantageous, as often data have been collected over prolonged temporal scales using standardised fishing methods. Additionally, these data can offer valuable insights into the biology and population ecology of large coastal shark species.

In KwaZulu-Natal (KZN), South Africa, the first shark nets were introduced in 1952, and, after a period of adjustment, the data collected by independent contractors were considered reliable from 1978 (Cliff and Dudley, 1992a). The KZN program is still in operation today, although sharks captured alive in nets are now tagged and released. Deceased sharks are retained, allowing for collection of long-term species-specific biological information which has resulted in a considerable number of peer-reviewed publications on the biology and ecology of a number of larger-bodied carcharhinids in this region (e.g. Cliff and Dudley, 1991; Cliff and Dudley, 1992a; Cliff and Dudley, 1992b; Dudley and Cliff, 1993; Smale and Cliff, 1998; Wintner and Dudley, 2000; Allen and Wintner, 2002; Cliff et al., 2002; Wintner et al., 2002; Dudley et al., 2005; Dudley and Simpfendorfer, 2006; Dudley and Cliff, 2010).

In Hawaii, periodic implementation and removal of shark control measures predominantly using longlines occurred in 1959 – 1960, 1966 – 1969, 1971 and 1976 (Wetherbee et al., 1994), usually initiated by either increases in human-shark interactions, or increased sightings of sharks around the main Hawaiian islands. Despite the majority of shark attacks involving *G. cuvier*, it was estimated that all

local shark populations had been reduced by as much as 50 – 90% after the moderate fishing effort of these control programs (Tester, 1969), however additional factors such as seasonality, weather and fishing effort were seldom considered in these estimates (Wetherbee et al., 1994). Due to the short-term duration of each of the control programs, annual and long-term changes in the population could not be monitored (Wetherbee et al., 1994). Nevertheless, the range of biological information obtained from ~ 4700 sharks over an 18-year period has also resulted in a comprehensive review of the biology of a range of large carcharhinids from Hawaiian waters (e.g. Polovina and Lau, 1993; Lowe et al., 1996; Holland et al., 1999; Lowe et al., 2006; Meyer et al., 2009; Meyer et al., 2010; Papastamatiou et al., 2013; Meyer et al., 2014).

In Australia, the New South Wales Shark Meshing Program (NSWSMP) began in 1949, and the Queensland Shark Control Program (QSCP) began in 1962. The NSWSMP utilises nets only, while the QSCP is the only program in the world to maintain both nets and baited drumlines. Until recently, sharks perceived to be potentially dangerous to humans caught in both programs were euthanased and disposed of at sea. However, the NSWSMP now routinely releases large sharks from nets if they are not moribund (Green et al., 2009). The majority of unprovoked shark attacks between 1990 – 2009 in Australia were attributed to *C. carcharias* (15 fatalities), compared with four fatalities attributed to *C. leucas* and three to *G. cuvier* (West, 2011). Although *C. carcharias* is responsible for the majority of human fatalities, *G. cuvier* is caught in the highest abundance each year in the QSCP (between 200 – 400), followed by *C. leucas* (between 50 – 150) and then *C. carcharias* (between 0 – 20) (Fisheries, 2006). The QSCP drumlines are highly selective for *G. cuvier* (91% of catch) while only 9% are caught in nets (Holmes et al., 2012). In the net-only NSWSMP the overall catch of these species is considerably less than in Queensland, with 49 *G. cuvier* and 110 *C. carcharias* caught between 1990 and 2010, and only 11 *C. leucas* caught between 1998 and 2010 (Reid et al., 2011).

Despite these long-standing programs being in place on the Australian east coast, equivalent peer-reviewed publications on large shark biology, compared with the South African and Hawaiian research, have been less forthcoming (e.g. Paterson, 1990; Simpfendorfer, 1992a; Krogh, 1994; Sumpton et al., 2010; Noriega et al., 2011; Werry et al., 2012). Both the QSCP and NSWSMP are managed by their respective state governments, with no formal sampling programs of deceased sharks currently in

place, leading to a paucity of biological data that may otherwise have been obtained from the thousands of sharks killed over the past 60 years. Shark contractors administering these programs currently record information relating to gear type, species caught, total length, sex, number of pups, predominant stomach contents, mortality state, net capture position, and weather and sea conditions. While these data are useful for catch, catch rate and basic biological information, their collection occurs at sea by non-scientific personnel and is likely to vary between contractors. Nevertheless, careful screening the data for readily identifiable species (e.g. *G. cuvier* and *C. carcharias*) can provide a critical fishery-independent monitoring tool (Dudley and Simpfendorfer, 2006).

1.6 THE TIGER SHARK (*GALEOCERDO CUVIER*)

Galeocerdo cuvier is the largest of the Carcharhinidae family, with a circumglobal distribution in both tropical and warm temperate coastal and pelagic waters. *G. cuvier* have been studied at various locations throughout their geographic range, including the Hawaiian Islands (Polovina and Lau, 1993; Lowe et al., 1996; Holland et al., 1999, the east coast of North America (Branstetter et al., 1987; Gallagher et al., 2011; Hammerschlag et al., 2013), the east coast of South Africa (Wintner and Dudley, 2000; Dicken and Hosking, 2009), Western Australia (Heithaus, 2001; Simpfendorfer et al., 2001; Wirsing et al., 2006), and the western Pacific region (Fitzpatrick et al., 2012b; Werry et al., 2014). Evidence suggests that *G. cuvier* are partial migrators, with some individuals moving large distances before returning to specific areas on a regular basis (Holland et al., 1999; Lea et al., 2015). In the western Pacific region, studies on the movement ecology of *G. cuvier* have been limited to the tropical waters of northern Australia (Fitzpatrick et al., 2012b) and New Caledonia (Werry et al., 2014), with limited information available regarding their movements in sub-tropical or seasonally warm-temperate waters. Seasonal habitat use is likely employed by tiger sharks as an important feeding strategy (Papastamatiou et al., 2006; Meyer et al., 2009), allowing individuals to exploit different prey areas (Meyer et al., 2009). As a partially migrating species, inter-annual variability in local abundances, particularly in seasonally warmer waters, may be considerable.

Despite tiger sharks having a global distribution, vertebral ageing studies of the species have thus far been conducted in Hawaii (De Crosta et al., 1984), the western North Atlantic (Kneebone et al., 2008), the Gulf of Mexico (Branstetter et al., 1987), and off the east coast of South Africa (Wintner and Dudley, 2000). Tiger shark growth has also been assessed through the use of mark-recapture methods in Hawaii (Meyer et al., 2014), western North Atlantic (Natanson et al., 1999; Kneebone et al., 2008), Western Australia (Wirsing et al., 2006), and off Brazil (Afonso et al., 2012), although low rates of recapture and a lack of representation of the species' full size range are generally limiting features of these studies (Meyer et al., 2014). Despite the ageing methods used, modelled estimates of the growth coefficient, k, and asymptotic total length, L_∞, appear to be markedly different for tiger sharks in different regions of the world. These observed differences in growth modelling may be due to studies having small samples sizes of the small and large individuals in a population, resulting in poor parameter estimates when the von Bertalanffy model is used (Cailliet and Goldman, 2004). More recent elasmobranch ageing studies have moved away from using t_0 (theoretical age at zero length) due to its lack of biological meaning, replacing the parameter with L_0 (length at birth) as a more robust method (Carlson and Baremore, 2003; Cailliet and Goldman, 2004). Despite the method used, identification of age and growth parameters at the population-level is needed to best inform local management of the species, highlighting the importance of region-specific studies being conducted.

Tiger sharks are the only carcharhinid with an aplacental viviparous (ovoviviparous) reproductive strategy (Whitney and Crow, 2007). While reproductive data on this species from Australian waters remain scant, selected aspects of tiger shark reproductive biology have been studied elsewhere. Size-at-maturity estimates are often based on the smallest recorded mature individual, ranging from 297 – 310 cm TL for females and 290 – 310 cm TL for males in the northwest Atlantic (Clarke and von Schmidt, 1965; Branstetter et al., 1987). In Africa, females are reportedly mature at 340 cm TL and males at 290 cm TL (Fourmanior, 1961; Wintner and Dudley, 2000; Aitken 2003). These findings were consistent with the maturity range for female (330 cm – 345 cm TL) and male (292 cm TL) tiger sharks in Hawaii (Whitney and Crow, 2007). Notwithstanding, reports of pregnant tiger sharks as small as 287 cm TL in northern Australia (Simpfendorfer, 1992a), and 210 cm TL in Brazil (Alves, 1977), indicate that there may be regional differences associated with the

species' reproductive strategy. Mean litter sizes reported at various locations range between 21 and 50 embryos per litter (Bigelow and Schroeder, 1948; Fourmanior, 1961; Rivera-López, 1970; Bass et al., 1975; Aitken, 2003; Whitney and Crow, 2007), although the relationship between the number of embryos and maternal length was found to be positively correlated in one study (Simpfendorfer, 1992a), but not others (Aitken 2003; Whitney and Crow, 2007). In order for quantitative stock assessments to be conducted, local information on reproductive parameters such as sex ratio at birth, number of offspring, maternal age or size, reproductive seasonality and cycle, and gestation period, are required for fishery assessment models (Walker, 2005).

Tiger sharks are thought to be more resilient to fishing pressure (Simpfendorfer, 1992a) in comparison to many other shark species, due to their relatively fast growth rates and large size at birth (Compagno et al., 2005). As a result, tiger shark numbers are believed to be stable or increasing in some locations, as suggested by previous localised studies on the Australian east coast (Simpfendorfer, 1992a; Chan, 2001) and in South Africa (Aitken, 2003; Dudley and Simpfendorfer, 2006). However, studies conducted at other locations indicate that local abundances may be affected by high levels of fishing pressure (Springer and Gilbert, 1963; Tester, 1969). In the northwest Atlantic, tiger shark catch rates have declined by an estimated 65% since 1986 (95% CI: 58 to 72%) (Baum et al., 2003). On the east coast of Australia tiger sharks are targeted by commercial and recreational fishers (Chan, 2001; Williams, 2002; Macbeth et al., 2009), by foreign vessels fishing illegally (Field et al., 2009), and through shark control programs (Paterson, 1990; Reid and Krogh, 1992). Despite the range of fisheries that interact with *G. cuvier*, a lack of species-specific reporting in most Australian commercial fisheries, coupled with the species' broad geographic distribution, movement capabilities and solitary nature, has made it difficult to determine accurate catch rate and population estimates. While tiger shark populations in tropical northeastern Australian waters appear stable (Simpfendorfer, 1992a), catch rate declines have been identified in the warm temperate regions of NSW (Park, 2009; Reid et al., 2011). The scale, duration and periodicity of movements of individual tiger sharks likely influences the inter-annual variability observed in local catch rates, particularly at higher latitude locations. Therefore, identifying the extent of resident versus migratory behaviour in these areas is imperative, particularly as catch rates are often used as a proxy for population abundance (Maunder and Punt, 2004; Lynch et al., 2012; Tavares et al., 2012).

Given the large size, semi-solitary nature, and broad-scale migrations of the tiger shark, widespread study of the biology and ecology of the species at the population level has been difficult. Further, apparent regional differences in biological parameters, such as growth rate, highlight the need for region-specific studies to be conducted (Natanson et al., 1999). Utilisation of specimens captured in shark control programs offer an opportunity for the biology of large, mature sharks to be analysed, as well as providing the long-term data to assess catch rate information and reproductive parameters such as gestation period and cycle. Future management regimes for apex predators like *G. cuvier* will benefit from quantitative stock assessments derived from local age, growth, and reproductive data.

1.7 AIMS OF THIS STUDY

This research project is the first of its kind on *G. cuvier* on the Australian east coast. Despite *G. cuvier* being the species most commonly caught by shark control programs on the east Australian coastline, published biological and ecological information available for this population remains scant. This study investigated the historical catch of *G. cuvier* through the QSCP to assess catch rates, average size and abundance of the species in Queensland waters over an 18 year period. Movement ecology of the species was then assessed through satellite tracking in order to contextualise the results of the catch rate analyses, and provide the first insight into the vertical habitat use of tiger sharks across the broader western Pacific Ocean. The research also provides the first detailed biological investigation of tiger sharks along the east Australian coast by assessing age, growth and reproduction.

The broad aims of this study were:

- To assess the long term spatial and temporal trends in QSCP *G. cuvier* catch rates and average size across nine tropical and sub-tropical locations along the Queensland coast (Chapter 2)

- To understand the movement and behavioural ecology of *G. cuvier* by using satellite tags to; 1) assess spatial dynamics, site fidelity and habitat use; 2) determine whether horizontal and vertical habitat use patterns vary according to shark size and/or sex; and 3), identify migratory paths and investigate *G. cuvier* connectivity across the western Pacific ocean (Chapter 3)

- To examine the age and growth rate of *G. cuvier* off the east coast of Australia using vertebral band pair analysis (Chapter 4)

- To investigate the reproductive biology of *G. cuvier* for the first time in Australian waters (Chapter 5)

CHAPTER 2: DECLINING TRENDS IN ANNUAL CATCH RATES OF THE TIGER SHARK (*GALEOCERDO CUVIER*) IN QUEENSLAND, AUSTRALIA

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Full length article

Declining trends in annual catch rates of the tiger shark (*Galeocerdo cuvier*) in Queensland, Australia

Bonnie J. Holmes[a,b,*], Wayne D. Sumpton[b], David G. Mayer[b], Ian R. Tibbetts[a], David T. Neil[c], Mike B. Bennett[d]

[a] School of Biological Sciences, The University of Queensland, St. Lucia Campus, Queensland 4072, Australia
[b] Fisheries Queensland, Department of Agriculture, Fisheries and Forestry (DAFF), Brisbane, Queensland 4001, Australia
[c] School of Geography, Planning and Environmental Management, The University of Queensland, St. Lucia Campus, Queensland 4072, Australia
[d] School of Biomedical Sciences, The University of Queensland, St. Lucia Campus, Queensland 4072, Australia

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ABSTRACT

Suitable long term species-specific catch rate and biological data are seldom available for large shark species, particularly where historical commercial logbook reporting has been poor. However, shark control programs can provide suitable data from gear that consistently fishes nearshore waters all year round. We present an analysis of the distribution of 4757 *Galeocerdo cuvier* caught in surface nets and on drumlines across 9 of the 10 locations of the Queensland Shark Control Program (QSCP) between 1993 and 2010. Standardised catch rates showed a significant decline ($p < 0.0001$) in southern Queensland locations for both gear types, which contrasts with studies at other locations where increases in tiger shark catch per unit effort (CPUE) have been reported. Significant temporal declines in the average size of tiger sharks occurred at four of the nine locations analysed ($p < 0.05$), which may be indicative of fishing reducing abundance in these areas. Given the long term nature of shark control programs along the Australian east coast, effects on local abundance should have been evident many years ago, which suggests that factors other than the effects of shark control programs have also contributed to the decline. While reductions in catch rate are consistent with a decline in tiger shark abundance, this interpretation should be made with caution, as the inter-annual CPUE varies considerably at most locations. Nevertheless, the overall downward trend, particularly in southern Queensland, indicates that current fishing pressures on the species may be unsustainable.

1. Introduction

Sharks are among the least understood marine vertebrate taxa (Camhi et al., 1998) which, in the case of large sharks, is often attributed to their elusive nature and natural low abundances (Stevens et al., 2000). Increased human exploitation over the past two decades, coupled with increasing habitat modification, pose immediate threats to shark populations worldwide (Cortés, 2000). Many species of sharks have low resilience to exploitation because of their life histories, often characterised by a late age at maturity and low fecundity (Musick et al., 2000). Clearly, accurate prediction of the ecological consequences of current and future population changes is critical for fisheries and ocean ecosystem management (Heithaus et al., 2007a). However, the vast geographic scale of pelagic marine ecosystems often constrains our ability to adequately monitor shark populations (Baum et al., 2003). Suitable long term species-specific data are often unavailable, with historical perspectives on original population sizes typically obscured by a reliance on recent data in analyses (Camhi et al., 1998; Baum and Myers, 2004).

The tiger shark, *Galeocerdo cuvier*, is a large apex predator widely distributed throughout the tropical and warm-temperate oceans of the world. Tiger sharks have been studied at various locations throughout their geographic range, including the Hawaiian Islands (Polovina and Lau, 1993; Lowe et al., 1996; Holland et al., 1999), the east coast of North America (Branstetter et al., 1987; Baum et al., 2003), the east coast of South Africa (Wintner and Dudley, 2000), and the western coast of Australia (Heithaus, 2001; Simpfendorfer et al., 2001; Heithaus and Dill, 2002; Wirsing et al., 2006). Evidence suggests that *G. cuvier* populations comprise, at least in part, of individuals that maintain large home ranges and return to specific areas on a regular basis (Holland et al., 1999; Heithaus, 2001). The cues for these migrations are thought to be increases in water temperature and alterations in prey abundance (Heithaus, 2001;

* Corresponding author at: C/o Bennett Lab, Rm 424, Level 4, Otto Hirschfeld Building, The University of Queensland, St. Lucia, Queensland 4072, Australia.
Tel.: +61 411 240 806.
E-mail address: b.holmes@uq.edu.au (B.J. Holmes).

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Heithaus and Dill, 2002; Meyer et al., 2009), although the degree to which each of these factors contribute to movement behaviours and habitat use remains unknown. Gradients in prey abundance may structure the distribution of tiger sharks, particularly since they exhibit ontogenetic dietary shifts (Lowe et al., 1996; Simpfendorfer et al., 2001). Known to exhibit cannibalism (Gudger, 1932; Meyer et al., 2009), the use by tiger sharks of particular areas may also be size-dependent, with smaller sharks occupying different habitats to larger sharks in order to avoid predation (Lowe et al., 1996). Indeed, it has been suggested that predator avoidance is a more important factor than habitat choice for juveniles (Heupel and Heuter, 2002).

In Australia, tiger sharks are present year-round in tropical/sub-tropical waters and occur seasonally south, to around Cape Naturaliste (33°30′S 115°00′E) in Western Australia, and to Merimbula (36°54′S 149°55′E) in New South Wales in late summer (Stevens and McLoughlin, 1991). Throughout their range in eastern Australia, tiger sharks are caught by commercial, recreational and game fishing sectors (Chan, 2001; Williams, 2002), and in bather protection programs in Queensland (DPI&F, 2006), and to a lesser extent, New South Wales (NSW) (Green et al., 2009). In the past 10 years, increases in illegal foreign fishing activity in northern Australian waters have occurred, mainly by small Indonesian vessels targeting large sharks for their fins (Griffiths et al., 2008, Field et al., 2009, Marshall, 2011). Large reductions in abundance are a standard outcome of fisheries exploitation, and are often coupled with range contraction (Worm and Tittensor, 2011). However, monitoring these declines adequately is often limited by lack of appropriate resources (White and Kyne, 2010) or, in more affluent countries such as Australia, the inherent low value of shark fisheries (Harry et al., 2011).

Despite tiger sharks being the most common species caught by the Queensland Shark Control Program (QSCP) (DPI&F, 2006), published biological and ecological information available for the population along the east coast of Australia is limited (Simpfendorfer, 1992). While there is currently no peer-reviewed literature available on the movement of tiger sharks in either the Indo-West or South Pacific regions, several long term tagging studies are currently underway. Research at other locations has provided evidence that tiger sharks are capable of large-scale oceanic movements (Heithaus et al., 2007b, in Western Australia; Meyer et al., 2010, in Hawaii), as well as evidence of site fidelity or 'residence' (Lowe et al., 2006 and Papastamatiou et al., 2010, in Hawaii) indicating that patterns of local abundance may differ among regions, and may be correlated with environmental factors such as water temperature and prey availability (Heithaus, 2001; Lowe et al., 2006; Meyer et al., 2010). Genetic work on the stock structure of tiger sharks within the Indo-Pacific basin is also in its infancy, but preliminary results suggest genetic partitioning of the population does exist (A. Bernard, pers. commun.).

Long term catch and catch rate trends for large sharks are difficult to obtain, and commercial logbook information has long been compromised by limited species-level reporting and inaccurate effort information. The use of shark control program information for deriving catch rate trends is advantageous, as often data have been collected over prolonged temporal scales using standardised fishing methods. As such, these data can provide a critical fishery-independent monitoring tool (Dudley and Simpfendorfer, 2006). Additionally, these data offer a valuable insight into the biology and population ecology of large coastal shark species. For example, in KwaZulu-Natal (KZN), South Africa, the first shark nets were introduced in 1952, and, after a period of adjustment, the data collected by independent contractors were considered reliable from 1978 (Cliff and Dudley, 1992). Subsequently, Dudley and Simpfendorfer (2006) conducted an analysis of the population status of 14 species of large sharks in the KZN region using a 26-year data set. Of the species assessed, only tiger sharks were found to have an increasing catch per unit effort (CPUE), with the authors suggesting that the increase in CPUE is indicative of an increase in tiger shark abundance over time.

In Australia, the New South Wales Shark Meshing Program (NSWSMP) began in 1949, and the Queensland Shark Control Program (QSCP) began 13 years later. Until recently, sharks perceived to be potentially dangerous to humans caught in both programs were euthanased and disposed of at sea. However, the NSWSMP now routinely releases large sharks from nets if they are not moribund (Green et al., 2009). Dudley (1997) analysed early NSWSMP catch records and reported initial declines in tiger shark catch rates after the program's inception, followed by subsequent increases in catch rates in the late 1980s. More recently, however, Reid et al. (2011) report that although the trend in CPUE is not statistically significant over the last 60 years investigated, a downward trend in CPUE in the past two decades implies a decrease in tiger shark abundance off NSW. Additionally, they report that a significant continual decrease in the proportion of large individuals across 20-year periods raises concern that current impacts on *G. cuvier* may be unsustainable. The only analysis of long term catch QSCP data for tiger sharks, undertaken at Townsville between 1964 and 1986, concluded that the abundance of *G. cuvier* may be increasing with no significant reduction in the mean size of sharks caught (Simpfendorfer, 1992). As these data were spatially limited, broader investigation of tiger shark life history parameters and catch rates are required, particularly in light of the recent downward trends reported in NSW. The current study presents an analysis of a long term spatial and temporal trends in QSCP tiger shark catch rates and average size across nine tropical and sub-tropical locations along the Queensland coastline. We examine the significant relationships between location, gear type, size and sex on catch rates of tiger sharks in order to investigate fluctuations in abundances over time.

2. Materials and methods

2.1. The Queensland Shark Control Program – study site and methods

The QSCP uses nets, drumlines, or a combination of both, positioned adjacent to popular bathing locations at 10 areas (85 beaches) along the Queensland coast (Fig. 1). A total of 348 drumlines and 35 nets are currently used in the program (Fig. 1). Surface mesh nets (186 m in length, 6 m drop, and 50 cm stretched mesh size) are predominantly set parallel, and approximately 500–1000 m, from shore (water depth 7–12 m). There are slight local variations depending on bathymetric conditions. Drumlines (usually a single 14/0 J hook) are likewise positioned 500–1000 m from the shore and baited with either mullet (*Mugil cephalus*) or shark flesh. In 2002 the use of frozen shark flesh as alternative bait was introduced in the QSCP amid increased reports of dolphin scavenging of mullet baits, particularly in the southern region. Currently the program uses both baits, and shark is used if dolphin pods are observed during rebaiting operations. Nets and drumlines are checked by contractors 15–20 days each month.

Fishing contractors record information relating to gear type, species caught, total length, sex, number of pups (if pregnant), stomach contents, whether sharks are dead or alive, the net position in which they are caught and weather and sea conditions. Although the program has been in operation since 1962, records (particularly relating to species identification and length measurement) within the program are considered reliable since 1993, following a review of the QSCP (Anon, 1992) that recommended a number of improvements including species identification training and protocols to improve data accuracy and precision. Historical tiger shark data are regarded among the most reliable, given

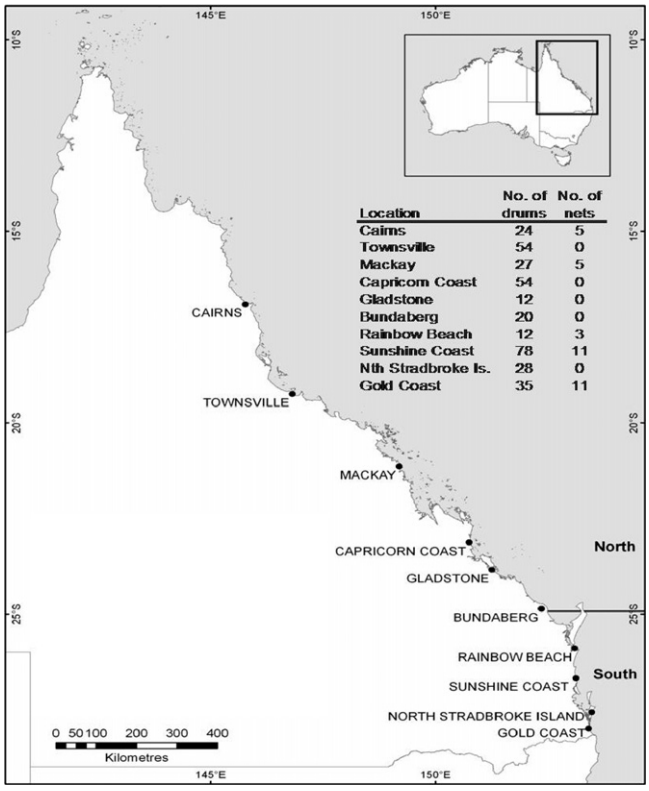

Fig. 1. Study area of Queensland showing the 10 locations of the Queensland Shark Control Program with gear details, and warmer northern (Bundaberg to Cairns) and cooler southern (Rainbow Beach to Gold Coast) Queensland regions.

the large vertical body stripes and blunt head shape that distinguish tiger sharks from other species and facilitate accurate identification. The fishing strategies in various locations have also changed dramatically since the program's inception, but fishing effort (numbers of nets and drumlines in each area) has remained relatively constant since 1993, except for the replacement of two nets at Townsville with drumlines in 1999 and an increase of four drumlines at North Stradbroke Island in 2006. Rainbow Beach was removed from the final CPUE analyses due to concerns about the data quality, and was not used in the catch rate results.

2.2. Statistical analyses

Catch rates were standardised across each location for gear types and fishing days, to catch per unit effort (CPUE, recorded as sharks net^{-1} day^{-1} or sharks $drumline^{-1}$ day^{-1}). Individual beaches were treated as samples within each location, with CPUE values pooled for each sex and size class at the gear type/month/year/location level. To account for the inflated numbers of zeros in the data, conditional or two-part generalised linear models (CGLMs) were used, in preference to mixture models. A binomial generalised linear model with the logit link (McCullagh and Nelder, 1989) was used to model the proportion of zeros. While a number of candidate discrete and continuous distributions are available to model the zero-truncated counts, the log-normal or gamma distributions are generally suitable for highly skewed continuous CPUE data (Ancelet et al., 2010). The gamma, with the log link, was adopted here, and the post-analysis residual plots indicated its suitability for these data. Both models were fitted using GenStat v12.1, with the resultant adjusted means from each then being combined (via multiplication) for presentation and interpretation. The standard formula for the variance of a product (Goodman, 1960) was used to calculate the relevant standard errors. Initial combined CGLMs indicated that gears were not directly comparable, as well as having different data coverage, therefore final models were conducted separately for the two gear types. The independent factors tested were year, month, location, sex, and size, and the respective interactions between them. This multi-factor exploratory analysis is valid in discerning the dominant patterns in the data, given the comprehensive coverage of the base data. Only effects which were significant ($p < 0.05$) in both the binomial and gamma models were retained. Year was initially fitted as a factor with discrete levels to indicate variability as well as trend, and where significant trends over years were found, a linear regression was fitted. To summarise differences in tiger shark biology and population structure between the tropics and subtropics, the means for locations were averaged into northern (Cairns to Bundaberg, >25°S) and southern (Sunshine Coast to Gold Coast, <25°S) regions (Fig. 1), where appropriate.

Total lengths of tiger sharks were analysed by linear regression against years. In order to reveal patterns of size and sexual segregation, males and females were divided into small (juvenile; <300 cm) and large (sub-adult and adult; >300 cm) groups. Sex ratio was analysed using a chi-squared test.

3. Results

Of 4757 tiger sharks caught from 1993 to 2010, the majority were captured on drumlines (91%) compared to nets (9%). Of these, 59% were female, 40% male and 1% were not sexed. The dominant effects in the CGLMs of drumline catches were the seasonal main effect, the location by year interaction, and the size by sex interaction (Table 1). Similarly, net catches had the same results except for the seasonal effect, where no trends were evident. Annual trends in CPUE for tiger sharks along the east coast of Queensland varied considerably among locations, and between the north (Cairns to Bundaberg) and the south (Sunshine Coast to Gold Coast) regions for both drumlines and nets (Table 2).

Trends in drumline CPUE differed significantly between locations and years, with the greatest declines observed on the Sunshine Coast, North Stradbroke Island and the Gold Coast, which make up the southern sub-tropical region. Similar declines of this magnitude were also recorded in Bundaberg ($R^2 = 0.637$, $p = <0.0001$), a location that straddles the sub-tropical south and tropical northern regions. Overall, a significant decrease in the catch rate of tiger sharks in the south was evident since 1993 ($R^2 = 0.888$, $p < 0.0001$) (Fig. 2). Drumline CPUE at Cairns and Gladstone in the tropical north was not significantly different over time. Other northern locations, however, did exhibit significant decreases over time, including Townsville ($R^2 = 0.238$, $p = 0.03$), Mackay ($R^2 = 0.498$, $p = 0.001$), and Capricorn Coast ($R^2 = 0.527$, $p = 0.0006$). A seasonal effect on drumline CPUE was significant in both regions ($p < 0.05$), where catch rates were highest during the cooler months (Apr–Aug) in northern Qld, and during the warmer months (Oct–Feb) in southern Qld.

Net CPUE was examined at Cairns and Mackay in the north, and at Sunshine Coast and the Gold Coast in the south. Due to fewer data, the standard errors were greater for the adjusted mean net CPUE compared with drumline CPUE. Cairns CPUE demonstrated the greatest decline in the north ($R^2 = 0.283$, $p = 0.0007$), with the catch rate in Mackay variable, but relatively stable (Fig. 3). The Sunshine Coast and Gold Coast locations in the south also had significant declines in mean net CPUE ($R^2 = 0.261$, $p < 0.0001$ and $R^2 = 0.363$, $p = 0.0001$, respectively).

The largest shark caught was a 550 cm total length (TL) female on the Capricorn Coast. The length frequency distributions of both males and females were unimodal, with both sexes commonly caught at 220–239 cm TL by both gear types (Fig. 4). Significantly

Table 1
Deviance ratio and probability results of the binomial and gamma model analysis by gear type for the fitted terms based on QSCP data from 1993 to 2010.

Fitted terms	Binomial model with logit link						Gamma model with log link					
	Drumlines			Nets			Drumlines			Nets		
	D.f.	Deviance ratio	Chi pr.	D.f.	Deviance ratio	Chi pr.	D.f.	Deviance ratio	F pr.	D.f.	Deviance ratio	F pr.
Year	17	6.88	<0.001	17	6.84	<0.001	17	6.69	<0.001	17	5.56	<0.001
Location	9	67.83	<0.001	4	61.29	<0.001	9	296.2	<0.001	4	127.29	<0.001
Size	1	697.12	<0.001	1	82.88	<0.001	1	214.36	<0.001	1	7.22	0.008
Month	11	1.5	0.123	11	1.58	0.096	11	6.91	<0.001	11	1.21	0.28
Sex	1	131.54	<0.001	1	1.29	0.256	1	27.73	<0.001	1	2.22	0.138
Location·Month	99	2.78	<0.001	44	1.44	0.029	98	1.4	0.007	41	0.85	0.732
Size·Month	11	5.98	<0.001	11	0.98	0.462	11	4.51	<0.001	11	0.74	0.703
Location·Size	9	9.54	<0.001	4	4.02	0.003	9	3.43	<0.001	4	0.21	0.935
Location·Sex	9	11.59	<0.001	4	2.72	0.028	9	1.88	0.051	4	3.38	0.011
Size·Sex	1	44.21	<0.001	1	0.16	0.688	1	0.07	0.79	1	0	0.968
Year·Location	153	2.9	<0.001	68	2.21	<0.001	150	1.58	<0.001	41	0.66	0.945
Year·Sex	17	1.92	0.012	17	1.21	0.244	17	1.61	0.055	17	0.7	0.797
Location·Size·Sex	9	3.22	<0.001	4	0.2	0.937	9	1.26	0.254	3	2.3	0.079
Residuals	8292			4132			2136			196		

more females than males were caught at most size classes except for sharks between 140 and 199 cm TL, and 260–279 cm TL. The sex ratio of the overall catch for drumline caught animals was significantly different from unity ($\chi^2 = 217$, df = 1, $p < 0.001$) at 1.52:1 female to male. The sex ratio for net caught tiger sharks was not significantly different at 1.17:1 ($\chi^2 = 0.98$, df = 1, $p > 0.05$). Significant temporal declines ($p < 0.05$) in the average size of tiger sharks occurred at four of the nine locations analysed (Table 2).

There was a significant interaction between size and year for modelled drumline and net catches, with a greater CPUE of small (<3 m) tiger sharks on both gear types (Fig. 5). For drumline catches of small and large (>3 m) sharks there was a significant difference between slopes ($p = 0.0005$), with a higher rate of decline in small sharks than large. This also occurred in net catches ($p = 0.05$) although to a lesser extent, primarily due to the lower number of tiger sharks captured in nets.

4. Discussion

Catch rates assessed in conjunction with appropriate biological and ecological characteristics of a species provide a better understanding of population trends than catch rate alone (Maunder et al., 2006). Shifts in length compositions to smaller sizes have been attributed to exploitation for a number of shark species (Anderson, 1985; Walker and Heessen, 1996; Rago et al., 1998; Bradshaw et al., 2008), while changes in the size structure may also be due to size-selective properties of fishing gear, particularly nets (Stevens et al., 2000). In Queensland, the average size of tiger sharks is stable or declining at eight of the nine locations (Table 2). Given that the NSW and southern QLD regions are towards the southern extent of the range for the species, the year-round fishing effort and current level of harvest may be contributing to a range contraction of the species. Recent downward catch rate trends reported in NSW (Reid et al., 2011), along with those reported here, also indicate a decrease in tiger shark abundance in the south.

Tiger sharks are thought to be more resilient to fishing pressure (Simpfendorfer, 1992) in comparison to many other shark species, due to their relatively fast growth rates and high juvenile survivorship (Compagno et al., 2005). As a result, tiger shark numbers are believed to be stable or increasing in some locations, as suggested by previous studies on the Australian east coast (Simpfendorfer, 1992; Chan, 2001) and in South Africa (Dudley and Simpfendorfer, 2006). However, studies conducted at other locations indicate that local abundances may be affected by high levels of fishing pressure (Springer, 1963; Tester, 1969; Baum et al., 2003). Concomitantly, shark control programs are considered effective because they reduce local populations of large shark species, including tiger sharks (Springer and Gilbert, 1963) which make up the majority of the catch in the QSCP (DPI&F, 2006).

Although catch rates were significantly higher in the northern part of the state, tiger sharks were caught in all 10 tropical and sub-tropical QSCP areas, indicating a cosmopolitan distribution

Table 2
Catch and catch per unit effort (CPUE) details for *Galeocerdo cuvier* at nine locations off the Queensland east coast based on QSCP data from 1993 to 2010.

Location	Gear selectivity				Mean annual catch (number)		Linear trends over time (years)					
	Drumlines		Nets				Drumline CPUE		Net CPUE		Mean total length (m)	
	Minimum size (cm TL)	Maximum size (cm TL)	Minimum size (cm TL)	Maximum size (cm TL)	♂	♀	R^2	Slope	R^2	Slope	R^2	Slope
Cairns	60	430	130	470	11.22	13.06	0.01	+0.004	0.28	−0.037**	0.64	−0.052**
Townsville	68	420	220	310	12.83	18.94	0.23	−0.015*	n/a	n/a	0.01	−0.002
Mackay	80	530	120	455	22.72	31.28	0.49	−0.038**	0.09	−0.049	0.32	+0.024*
Capricorn Coast	40	550	n/a	n/a	15.56	12.56	0.52	−0.016**	n/a	n/a	0.02	−0.009
Gladstone	100	435	n/a	n/a	3.39	7.00	0.04	−0.008	n/a	n/a	0.38	−0.047**
Bundaberg	70	455	n/a	n/a	12.72	26.28	0.63	−0.069**	n/a	n/a	0.26	−0.023*
Sunshine Coast	50	450	100	410	10.00	24.00	0.69	−2E−05**	0.26	−0.018**	0.08	−0.020
North Stradbroke Is.	70	460	n/a	n/a	2.11	8.06	0.58	−2E−05**	n/a	n/a	0.04	−0.022
Gold Coast	100	420	210	360	6.11	6.72	0.85	−4E−05**	0.36	−0.011**	0.47	−0.097**

R^2, fit of data, n/a = nets not at this location.
* $p < 0.05$.
** $p < 0.01$.

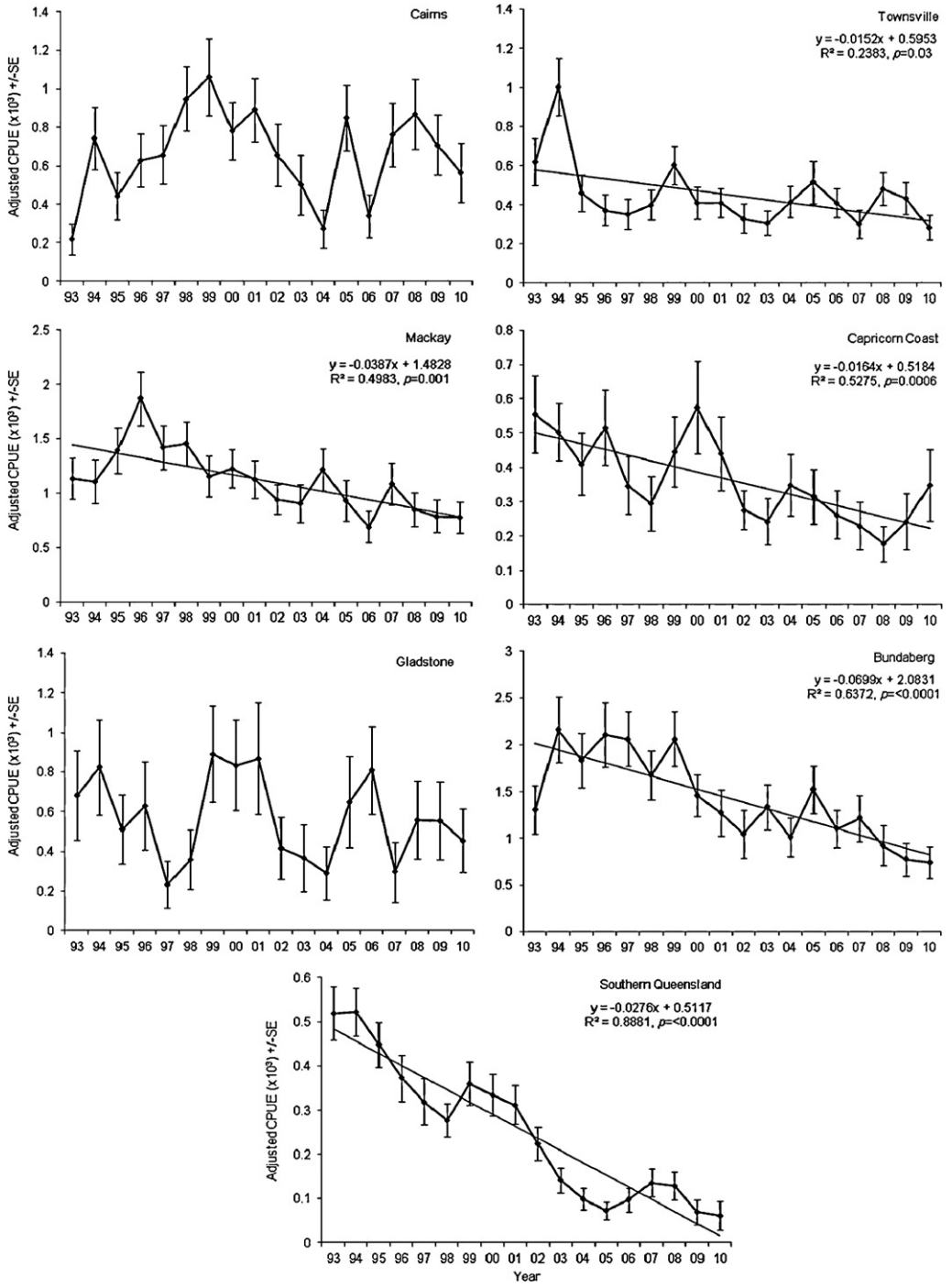

Fig. 2. Mean annual adjusted drumline CPUE (number drumline^{-1} day^{-1}) and trend lines (where significant) for the nine QSCP locations from 1993 to 2010. Locations in southern Qld (Sunshine Coast, North Stradbroke Island, Gold Coast) were grouped as all displayed a significant decline in CPUE (refer to Table 1). Rainbow Beach was data deficient and not included in the analysis.

along the coastline. Increases in abundance in southern waters appear to occur during the warmer months. However, it is unclear whether this seasonal effect is a result of regular large-scale migrations of tiger sharks from the north and/or from movements to the nearshore environment from offshore shelf waters (Holmes et al., unpublished data). As reported elsewhere, tiger shark movements are likely to be related to prey availability and fluctuations in water temperature (Heithaus, 2001; Lowe et al., 2006; Meyer et al., 2010), and these factors may influence observed catch rates at a local scale. Interestingly, the difference in catch trends between regions suggests that some level of mesoscale stock structuring is present.

Simpfendorfer (1992) reported QSCP tiger shark catch rates from the Townsville region for the 1964–1986 period and found relatively stable catch rates. He also reported no change in the mean size of males and only a small reduction in the mean size of females, concluding that this species was probably resilient to moderate fishing pressure at that location (Simpfendorfer, 1992). We now present evidence of a significant decline in catch rates of tiger sharks in Townsville ($p = 0.03$). However the size of sharks captured at that location still remains relatively stable. While reductions in catch rate are consistent with a decline in tiger shark abundance, cautious interpretation is warranted given the significant inter-annual

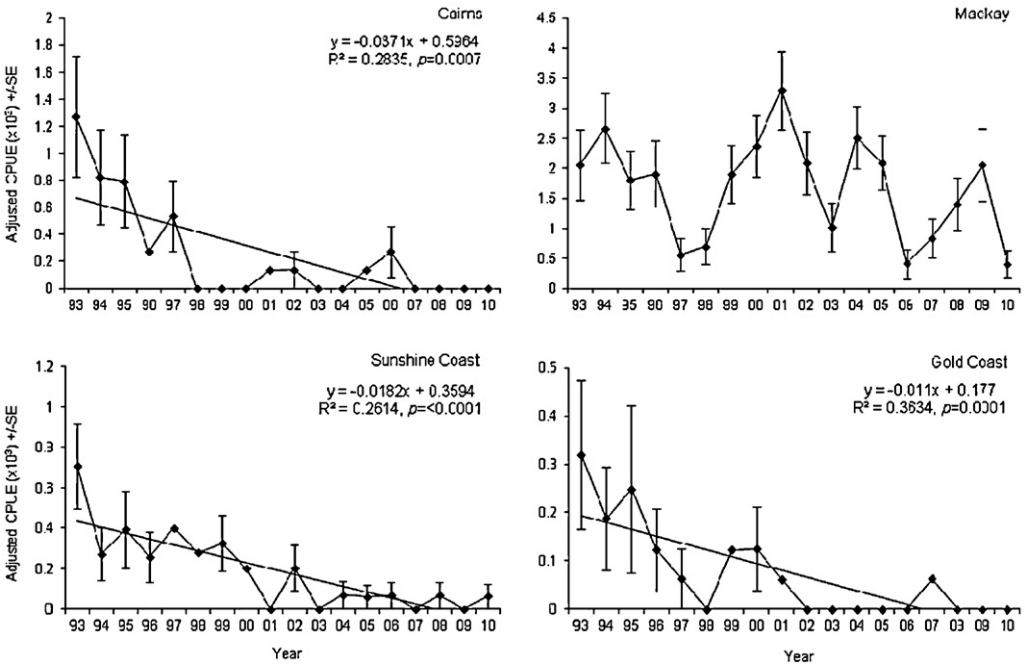

Fig. 3. Mean annual adjusted net CPUE (number net^{-1} day^{-1}) for the northern (Cairns and Mackay) and southern (Sunshine and Gold Coast) regions. Townsville and Rainbow Beach nets removed from analysis due to insufficient data.

variation in CPUE at most locations. Further to this, interpretation of the regional data in isolation, particularly those for net caught tiger sharks, would result in quite different conclusions than those derived by examining the full range of data from all locations.

The significant rates of CPUE decline ($p < 0.0001$) occurring in both nets and on drumlines in southern Queensland are consistent with other studies in the same region for some carcharhinids (e.g. bull sharks; Werry, 2010), but not others (e.g. spinner sharks; Sumpton et al., 2010) suggesting that other external influences on local abundance may occur. Given the long term nature of the QSCP it is reasonable to assume that localised depletions of 'resident' sharks should have stabilised catch rates many decades prior to 1993, with only steady harvesting of 'migrants' occurring (Dudley, 1996). In the KZN shark control program, tiger sharks are the only species with an increasing CPUE, with the authors suggesting that their life history is better suited to sustained catches than other shark species (Dudley and Simpfendorfer, 2006). It should be noted, however, that the KZN shark control program releases all healthy live tiger sharks (42% of the total tiger shark catch, between 1989 and 2003), which is not a standard practice of the QSCP. In addition, we have shown that drumlines strongly select for tiger sharks, while nets do not. As both the KZN and NSW programs use nets only, it is conceivable that by comparison the historically higher levels of drumline catch and euthanizing tiger sharks in the QSCP has had a greater impact on the species' sustainability in Queensland. Other factors in addition to the effects of the QSCP fishing operations, including recent increases in commercial and recreational shark fishing in Queensland (Williams, 2002; Harry et al., 2011), NSW (Macbeth et al., 2009) and beyond state waters (Marshall, 2011) are also likely contributing to the observed catch rate declines.

The use of frozen shark flesh as an alternative bait to mullet reduces dolphin scavenging, allowing drumlines to actively 'fish' for longer periods. The scavenging of mullet baits has likely reduced the effectiveness of the drumlines on some shark species. However, several studies have demonstrated that tiger sharks are generalist feeders and may show preference for elasmobranchs in their diet (Lowe et al., 1996; Simpfendorfer et al., 2001). The possible effect of a change in baits on the observed catch rates could not be quantified as bait type per drumline is not recorded in contractor logbooks. Nevertheless, the observed declines in catch rates of tiger sharks

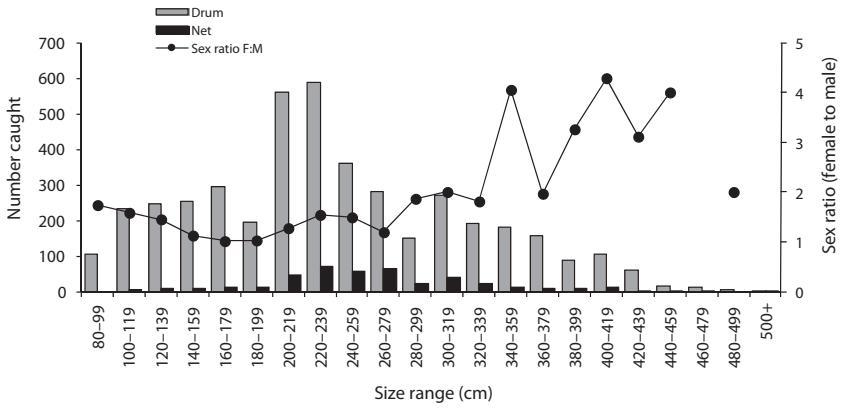

Fig. 4. Size range of tiger sharks caught in nets and on drumlines in the QSCP throughout Queensland 1993–2010. Sex ratio (female to male) for each size class also shown.

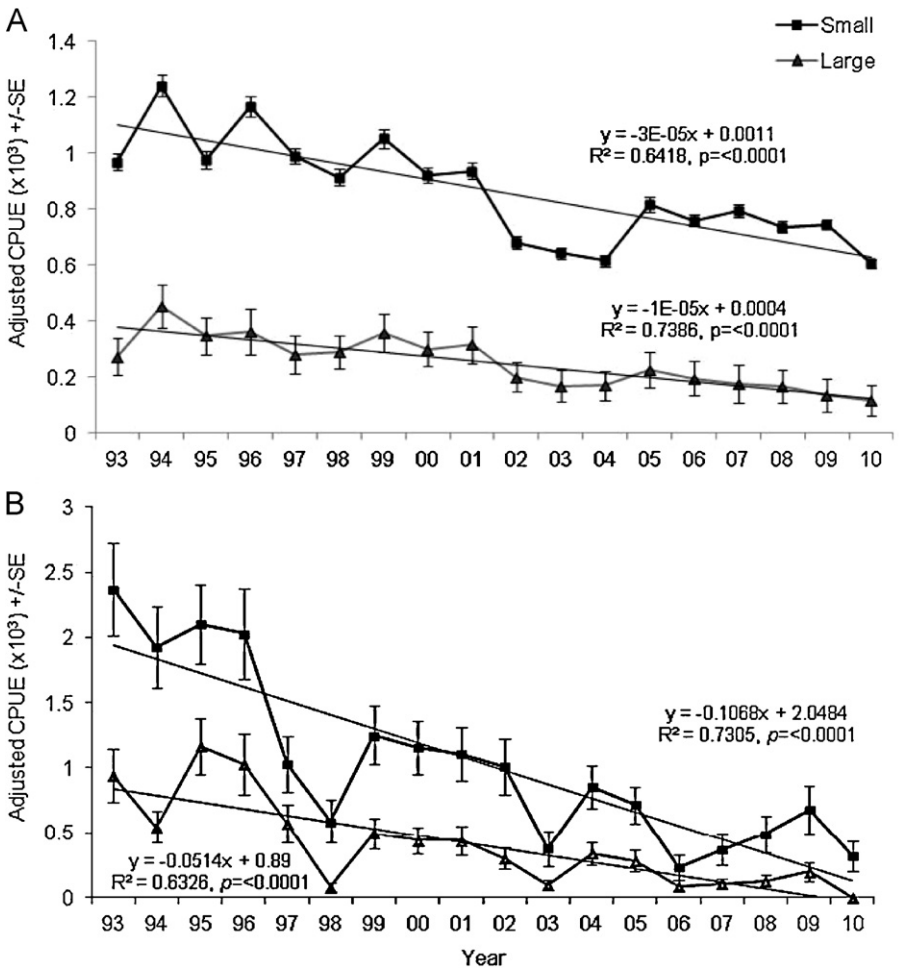

Fig. 5. Catch rates (number gear^{-1} day^{-1}) by year and size of tiger sharks on (A) drumlines, and in (B) nets by the QSCP between 1993 and 2010.

on drumlines were paralleled by a decline in catch rates in nets deployed in the same regions, which suggests that declines are not likely to be related to changes in the efficiency of fishing gear. A similar decline in tiger shark catch rates in the NSWSMP in recent years (Reid et al., 2011) is consistent with these observations of QSCP net catches in southern Queensland waters.

Increasing human population growth has contributed to the significant degradation of fish habitats in southeast Queensland, and commercial and recreational fishing pressures are also several orders of magnitude higher than other areas of the Queensland coast (McInnes, 2008; Meynecke et al., 2008). Secondary impacts of the harvest of prey items of large sharks are likely, though difficult to quantify. The commercial catch of tiger sharks in Queensland occurs predominantly in the north of the state (DEEDI, 2011), and given this species' potential for large-scale movement, extraction in the tropics may reduce the number that seasonally move to the south. It is also noteworthy that a significant commercial harvest also exists in northern NSW through both commercial and game fishing activities (Chan, 2001; Macbeth et al., 2009) putting further pressure on sharks that potentially visit or move through southern Queensland waters. Consequently, a greater understanding of the level of population connectivity and movement behaviour of tiger sharks in the east Australian and South Pacific region is important for assessing the longer term effects of fisheries and programs such as the QSCP. With possible range contraction occurring, further research to describe the scale, duration and periodicity of movements in migratory individuals compared with the behaviour of animals that might be considered resident, are required to determine whether reductions in CPUE and shark length in fishery-independent programs like the QSCP are indicative of population level changes in abundance.

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CHAPTER 3: TIGER SHARK (*GALEOCERDO CUVIER*) MOVEMENT PATTERNS AND HABITAT USE DETERMINED BY SATELLITE TAGGING IN EASTERN AUSTRALIAN WATERS

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ORIGINAL PAPER

Tiger shark (*Galeocerdo cuvier*) movement patterns and habitat use determined by satellite tagging in eastern Australian waters

Bonnie J. Holmes · Julian G. Pepperell · Shane P. Griffiths · Fabrice R. A. Jaine · Ian R. Tibbetts · Mike B. Bennett

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Abstract Partial migration is considered ubiquitous among vertebrates, but little is known about the movements of oceanodromous apex predators such as sharks, particularly at their range extents. PAT-Mk10 and SPOT5 electronic tags were used to investigate tiger shark (*Galeocerdo cuvier*) spatial dynamics, site fidelity and habitat use off eastern Australia between April 2007 and May 2013. Of the 18 tags deployed, 15 recorded information on depth and/or temperature, and horizontal movements. Tracking times ranged between four and 408 days, with two recovered pop-up archival tags allowing 63 days of high-resolution archived data to be analysed. Overall mean proportions of time-at-depth revealed that *G. cuvier* spent the majority of time-at-depths of <20 m, but undertook dives as deep as 920 m. Tagged sharks occupied ambient water temperatures from 29.5 °C at the surface to 5.9 °C at depth. Deep dives (>500 m) occurred mostly around dawn and dusk, but no definitive daily dive patterns were observed. Horizontal movements were characterised by combinations of resident and transient behaviour that coincided with seasonal changes in water temperature. While the majority of movement activity was focused around continental slope waters, large-scale migration was evident with one individual moving from offshore Sydney, Australia, to New Caledonia (*c*. 1,800 km) in 48 days. Periods of tiger shark residency outside of Australia's fisheries management zones highlight the potential vulnerability of the species to unregulated fisheries and the importance of cross-jurisdictional arrangements for species' management and conservation.

Introduction

An understanding of spatio-temporal movements of animals is of central importance when assessing the dynamics

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B. J. Holmes (✉)
School of Biological Sciences, The University of Queensland, Rm 424, Otto Hirschfeld Building, St Lucia, QLD 4072, Australia
e-mail: b.holmes@uq.edu.au

J. G. Pepperell
Pepperell Research and Consulting Pty Ltd, PO Box 1475, Noosaville BC, QLD 4566, Australia

S. P. Griffiths
CSIRO Oceans and Atmosphere Flagship, GPO Box 2583, Brisbane, QLD 4001, Australia

F. R. A. Jaine
Biophysical Oceanography Group, School of Geography, Planning and Environmental Management, The University of Queensland, Chamberlain Building, St Lucia, QLD 4072, Australia

F. R. A. Jaine
Manta Ray and Whale Shark Research Centre, Marine Megafauna Foundation, Casa Barry Lodge, Tofo Beach, Mozambique

I. R. Tibbetts
School of Biological Sciences, The University of Queensland, Goddard Building, St Lucia, QLD 4072, Australia

M. B. Bennett
School of Biomedical Sciences, The University of Queensland, Otto Hirschfeld Building, St Lucia, QLD 4072, Australia

and interactions within and between populations (Skov et al. 2010). Migration is a specific type of movement that may be persistent or seasonal, often featuring highly directional, long-distance travel (Dingle and Drake 2007; Papastamatiou et al. 2013). Acting at multiple scales, animal migration may influence population structure, govern ecosystem dynamics and influence evolutionary processes and patterns of local and global biodiversity (Nathan et al. 2008). However, in most animal populations, only a proportion of the population migrates—where individuals display either a resident or migrant behaviour—a process known as partial migration (Skov et al. 2010; Broderson et al. 2011; Chapman et al. 2011). In addition to the well-studied variation among species and between populations within a species, often there is within-population migratory behavioural variation that is seldom considered (Chapman et al. 2011). In a growing number of examples, individuals within populations show differences in migratory behaviour, with some individuals migrating between habitats while others remain resident in a single habitat (Dingle 1996).

With recent advances in tagging technology, our capacity to follow the individual movements of animals has led to the growing observation of partial migration and the factors driving it, particularly in aquatic species (Skov et al. 2010; Papastamatiou et al. 2013). These factors include environmental conditions, resource partitioning, ontogenetic diet shift, body condition, reproductive state and predation vulnerability (Chapman et al. 2011; Papastamatiou et al. 2013). As a result, both the timing of migration and the resident/migratory fraction in partially migrating populations are likely to vary between years and between populations (Cagnacci et al. 2011; Mysterud et al. 2011; Broderson et al. 2011). Within aquatic communities, recent studies suggest that all groups of fishes demonstrate partial migration, including oceanodromous top predators such as sharks (Chapman et al. 2012; Papastamatiou et al. 2013). Indeed, the partial migration of predatory elasmobranchs, whose movement patterns may be shaped by the dynamics of the surrounding environment, will have consequences for ecological processes and may influence fisheries management and conservation strategies (Forchhammer et al. 2002; Papastamatiou et al. 2013).

The global decline in shark populations due to overfishing has been documented extensively (Baum et al. 2003; Myers et al. 2007; Lam and Sadovy de Mitcheson 2011; Dulvy et al. 2013). However, the scale of commercial, artisanal and illegal fishing practices differs greatly among oceanic regions. More recently, the implementation of marine protected areas (MPAs) has been successful in reducing shark population declines in some areas (Dulvy et al. 2006; Bond et al. 2012; da Silva et al. 2013), but these areas seldom encompass the full home range of larger shark species (Knip et al. 2012). The southwest Pacific Ocean, comprising the east coast of Australia, New Zealand and many South Pacific Islands, encompasses a complex of exclusive economic zones (EEZ) and territorial sea and archipelago waters interspersed with international high seas. The lack of fishing regulation in international waters, coupled with the vastly different management and monitoring regimes of neighbouring jurisdictions, such as areas in the southwest Pacific, has resulted in increased threats to migratory shark species (Dulvy et al. 2008).

The tiger shark, *Galeocerdo cuvier* (Péron and Lesueur 1822), is a cosmopolitan species that occurs throughout the tropical and warm-temperate coastal and epipelagic waters of the world (Last and Stevens 2009). Currently listed as 'Near Threatened' on the International Union for the Conservation of Nature's (IUCN) Red List of Threatened Species (Simpfendorfer 2009), *G. cuvier* can grow to around 550 cm total length (TL) and is the largest species in the family Carcharhinidae (Meyer et al. 2014). As an apex predator, tiger sharks have the ability to exert top-down pressure on marine ecosystems (Heithaus et al. 2008), such that the timing and extent of their movements may affect both population and trophic dynamics across a range of habitats (Skov et al. 2010). Studies of tiger sharks at various locations around the world have reported long-distance movements across the open ocean (Holland et al. 1999; Heithaus et al. 2007; Hammerschlag et al. 2012; Werry et al. 2014) and have revealed that individuals return to specific areas on a regular basis (Lowe et al. 2006; Fitzpatrick et al. 2012). Such site fidelity by some shark species has been attributed to foraging (Meyer et al. 2009), mating (Pratt and Carrier 2001), parturition (Baker et al. 1995) and the use of natal nurseries (Knip et al. 2012). In addition, habitat use may be related to size, with smaller sharks occupying different habitats to larger sharks in order to avoid predation (Lowe et al. 1996). As tiger sharks mature, their movements presumably include elements of exploration that enable them to discover new foraging grounds over time (Meyer et al. 2009). Holland et al. (1999) concluded that individual tiger sharks in Hawaii routinely utilised certain long-distance 'travel paths'. At high latitudes, seasonal migrations have also been identified (Heithaus 2001; Wirsing et al. 2006). The drivers for these migrations are thought to be changes in water temperature and prey abundance, although the degree to which each of these factors contribute to movement behaviours and habitat use is unknown (Heithaus et al. 2001; Heithaus and Dill 2002; Meyer et al. 2009). More recently, Papastamatiou et al. (2013) surmised that tiger sharks in Hawaii are discretionary partial migrators that use conditional strategies based on both fixed intrinsic states (i.e. age and sex) and flexible extrinsic states (i.e. prey abundance and water temperature) to determine habitat use. However, the study concluded that using horizontal movement data alone could not verify the factors that drive partial migration and that collection of other behavioural data were needed.

On the east coast of Australia, tiger sharks occur seasonally to Merimbula (36°54′S 149°55′E) in southern

New South Wales (NSW) during late summer (Last and Stevens 2009). Water conditions during these warmer months are characterised by increased surface flow over the continental shelf by the southward-flowing East Australian Current (EAC), with deeper thermoclines (50–200 m) and stronger eddies into the Coral and Tasman seas (Ridgway and Godfrey 1997; Steinberg 2007). Tiger sharks in these waters are targeted by commercial and recreational fishers (Chan 2001; Williams 2002; Macbeth et al. 2009), as well as by foreign vessels fishing illegally (Field et al. 2009). Governmental 'culling' operations through managed shark control programmes have also been in place at selected coastal regions of Queensland (QLD) and NSW for over 50 years (Paterson 1990; Reid and Krough 1992). Despite the range of fisheries that interact with *G. cuvier*, a lack of species-specific reporting in most Australian commercial fisheries, coupled with the species' broad geographic distribution, movement capabilities and solitary nature, has made it difficult to determine accurate catch rate and population estimates. While tiger shark populations in tropical north-eastern Australian waters appear stable (Simpfendorfer 1992; Holmes et al. 2012), catch rate declines have been identified in the southern subtropical QLD and warm-temperate regions of NSW (Park 2007; Reid et al. 2011; Holmes et al. 2012). The scale, duration and periodicity of movements of individual tiger sharks likely influence the inter-annual variability observed in local catch rates, particularly at higher-latitude locations (Holmes et al. 2012). Therefore, identifying the extent of resident versus migratory behaviour in these areas is imperative, particularly as catch rates are often used as a proxy for population abundance (Maunder and Punt 2004; Lynch et al. 2012; Tavares et al. 2012). Further, collection of biological and environmental data may identify the intrinsic (i.e. sex and age) and extrinsic (i.e. water temperature) factors needed to develop future population models, better interpret catch rate data and implement region-specific conservation initiatives in the future.

To better understand the movement and behavioural ecology of tiger sharks on the east coast of Australia, the objectives of this study were to: (1) assess tiger shark spatial dynamics, site fidelity and habitat use off eastern Australia, (2) determine whether horizontal and vertical habitat use patterns vary according to shark size and/or sex and (3) identify migratory paths and investigate tiger shark connectivity across the broader western Pacific Ocean.

Materials and methods

Study sites

Tiger sharks were captured for tagging in both nearshore and offshore shelf waters at a number of locations throughout south-eastern Australia between April 2007 and April 2012. In QLD, tagging locations included the Sunshine Coast (25° 52′S 152°33′E), Bundaberg (24°30′S 153°15′E) and one location further north at Batt Reef (16°23′S 145°46′E) on the Great Barrier Reef. In NSW, tiger sharks were tagged at four locations on the Central Coast (33°17′S 151°11′E) and at two locations on the South Coast (34°35′S 150°52′E) (Fig. 1).

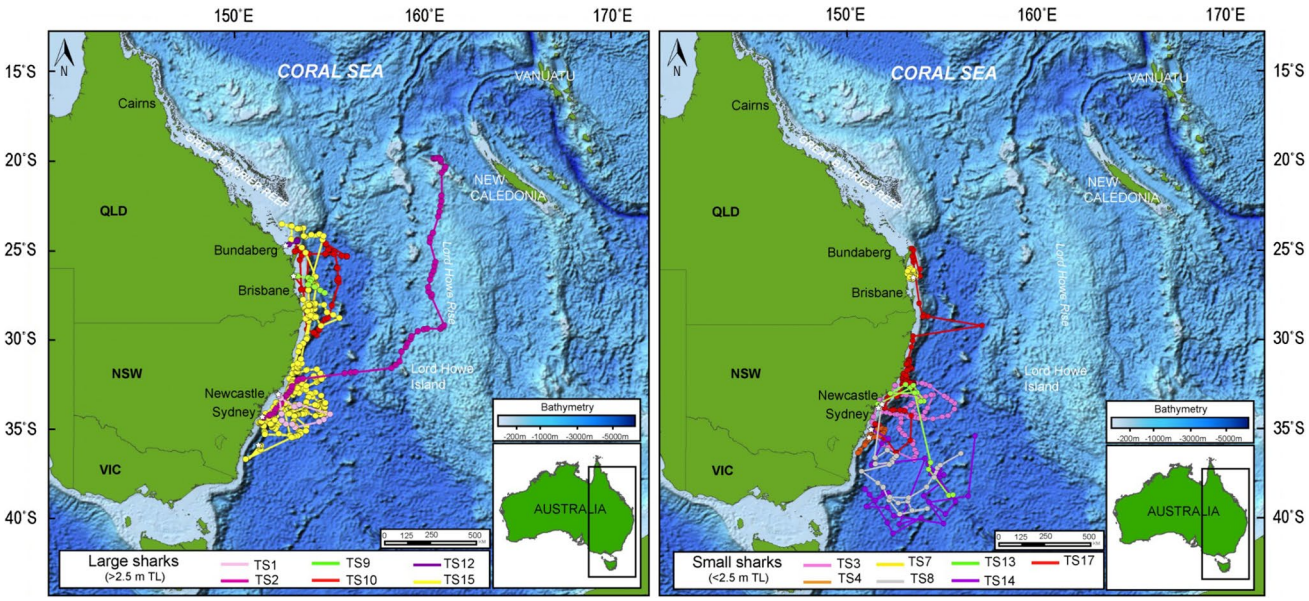

Fig. 1 Study site on the east coast of Australia. Individual tracks of tiger sharks are plotted by large (>2.5 m TL) and small (<2.5 m TL) animals. Tagging locations indicated by *white stars*

Specimen capture and electronic tagging

Sharks in nearshore waters were captured using single 18/0 J-hook drumlines baited with either mullet (*Mugil cephalus*) or unidentified shark flesh. Tiger sharks in offshore waters were attracted using chum (mixed fish mince) and captured on rod and line equipped with a single 10/0 tuna circle hook baited with an oily fish such as small mackerel tuna (*Euthynnus affinis*) or bonito (*Sarda australis*). Captured sharks were secured in a head-forward position next to the vessel and secured by a tail rope to ensure the animals remained close to the boat in preparation for tagging. An additional rope was also secured immediately posterior to the pectoral fins. A slow forward boat speed of 1 kn was maintained to ensure that water continued to pass over and the gills to oxygenate the blood. Total length (TL), fork length (FL), pre-caudal length (PCL), sex, tagging location, time and sea surface temperature (SST) were recorded for each shark.

Two types of electronic tags were used to track the movements and habitat utilisation of tiger sharks: the Wildlife Computers Mk10 Pop-up Archival Tag (PAT) and the Smart Position and Temperature Transmitting Tag (SPOT5). A 40-cm hand-held tagging pole was used to attach the PAT to the shark lateral to the base of the dorsal fin. Each PAT was tethered by two 6-cm strands of 135 lb nylon-coated stainless steel leader, crimped to a SPRO heavy swivel and attached to a 5-cm stainless steel dart head that was inserted into the dorsal musculature of the shark. Crimps were further covered using blue heat-shrink plastic tubing. SPOT5s were fitted to the upper portion of the first dorsal fin using nylon bolts passed through the fin and secured with stainless steel nuts. These tags were fitted so that the wet/dry sensor was out of the water when the upper dorsal fin broke the surface of the water.

Tag programming

All PATs were programmed to release after 180 days and then transmit archived data to the Argos system of polar orbiting satellites (www.argos-system.org). Time-at-temperature (°C) and time-at-depth (m) histograms were programmed in 14 user-defined bins. Temperature was measured in 2 °C increments from 6 to >30 °C (resolution = 0.05 °C; accuracy = ±0.1 °C), while depth was measured from 0 m to >1,000 m (resolution = 0.5 m; accuracy = ±1 m for 0–100 m range, ±1 % of reading for 100–1,000 m range). Each tag was programmed to record ambient light, temperature and depth at 10-s intervals. Although these tags could only deliver data aggregated over 4-hourly periods for the specified data bins via the Argos satellites, the entire high-resolution data record could be retrieved from recovered tags. A premature release mechanism was programmed to indicate a mortality event, whereby the tag would detach from the tether if the tag recorded a constant depth (±2 m) for a period greater than 96 h. For the SPOT5s, temperature (°C) was recorded in 12 bins in 2.5 °C increments from <5 to >32 °C. Tags were programmed to transmit location and temperature data to Argos satellites whenever the tag was exposed to the air when the shark was on the surface.

Data analyses

Igor Pro V6.22A and R V2.15.1 (R Core Team 2012) were used to plot vertical habitat use against temperature. Daily positions for PATs were estimated from raw ambient light data using the Wildlife Computers Global Position Estimator (WC-GPE) software (www.wildlifecomputers.com). Dawn/dusk light-level data were extracted using Wildlife Computers Argos Message Processor (WC-AMP), and daily latitudes and longitudes were estimated using WC-GPE. Daily records with poor dawn/dusk light-level curves were excluded from the analyses. Daily positions were estimated using an unscented Kalman filter (UKF), a state-space model applied to light-level measurements using R statistical software (Lam et al. 2008). Position estimates can be improved by matching sea surface temperature (SST) recorded by a tag when near the surface with remotely sensed SST data (Nielsen et al. 2006). Although this was undertaken for our tags, it proved unsuccessful either in improving position estimates or even reducing the variance around the light-only estimates. The reconstruction of movement tracks derived from the position estimates from light-only data was plotted using ArcGIS 10 (www.esri.com). Tracks were then regularized to one position per day to reduce variability associated with temporal frequency of positions (Aebischer et al. 1993), and kernel density was calculated to observe habitat use in ArcGIS [spatial analyst/kernel density]. Step lengths were calculated using geodetic distances calculated in R (Jaine 2013). Rate of movement (ROM) was calculated by dividing step length (in kilometres) between pairs of mean estimated positions by the time (in hours) between position fixes.

Tiger shark diel movements were examined using binned depth data collected by the PAT deployments. Data bins comprised 4 h of recorded information starting at 2000, 0000 hours (midnight), 0400, 0800, 1200 hours (midday) and 1600 hours. Some day/night overlap occurred between the approximate hours of 0400–0600 hours in the morning and 1600–1800 hours in the evening, depending on the time of year. In order to further adjust for potential errors associated with the overlap periods, day/night graphs of depth and temperature were plotted using Igor Pro software. A fast Fourier transform (FFT) analysis was conducted on the full archive data

from recovered tags to examine diel periodicity in vertical movements within the water column.

For the SPOT5s, the position of the tag was determined during each transmission by the Argos satellite system. The accuracy of position estimates is reported in seven location classes (LC) of 3, 2, 1, 0, A, B and Z, with LC3 the most reliable (error <250 m), while LC2 = 250–500 m, LC1 = 500–1,500 m, LC0 to LCB = >1,500 m, LCZ = no position (CLS 2011). Position fixes were used from location data with a LC of 3–1 only. Movement and kernel density data were calculated using the same method applied to PATs. Individuals were separated into large (>2.5 m TL) and small (<2.5 m TL) sharks on map plots to establish horizontal movement patterns in relation to size. The magnitude and distribution of errors from Kalman filter location estimates have been assessed previously, with modelled PAT data providing comparable geolocation estimates to SPOT5 data (Holdsworth et al. 2009; Sippel et al. 2011). As such, kernel density is presented as a percentage of daily average positions for all sharks, with the 95 and 75 % contours highlighting core regions of occupancy.

Results

Tag deployments

A total of 18 tiger sharks were tagged with either PATs or SPOT5s off the coastal areas of QLD and NSW (Fig. 1; Table 1). Of these, two appeared lethargic at release (TS#16 and TS#18) and were subsequently presumed to have died as the deployed SPOT5s did not transmit. In addition, despite the release of TS#11 in apparently healthy condition, the deployed PAT failed to transmit. TS#9 appeared to have died after 5 days at liberty as the depth profile indicated a dive of over 1,760 m for longer than 96 h, prompting the premature release of the PAT. Of the 15 tagged sharks yielding data, geolocation maps were estimated for

Table 1 Summary of shark biological details and tag deployments for *Galeocerdo cuvier* off of eastern Australia

Shark ID	Sex	Total length (cm)	Date tagged	Tag type	Days at liberty	Track length (km)	Mean step length (km day^{-1})	Mean speed (km hour^{-1})	Max depth (m)	Min temp (°C)
TS#1	M	310	17/04/07	PAT	14	798	66.5	3.8	672	7
TS#2	F	320	5/05/07	PAT	48	2,431	41.2	2.1	920	6
TS#3	F	200	18/11/07	PAT	58[a]	2,485	36.6	2.6	872	5.9
TS#4	F	165	24/11/07	PAT	11	320	16.9	1.1	328	7
TS#5	F	350	2/02/08	PAT	4	–	–	–	512	12
TS#6	F	335	5/04/08	PAT	5[a]	–	–	–	382	12.8
TS#18	F	230	2/07/09	SPOT	–	–	–	–	–	–
TS#7	M	180	22/07/09	SPOT	103	649	14.8	1.4	n/a	7.6
TS#8	F	152	10/04/10	PAT	12	1,923	80.1	3.4	336	19
TS#9	F	310	25/09/10	PAT	9	258	32.3	3.0	156	20.6
TS#10	F	290	25/03/11	SPOT	165	1,980	46.0	4.1	n/a	12.9
TS#11	F	175	24/04/11	PAT	–	–	–	–	–	–
TS#12	F	260	24/07/11	PAT	6	2.5	0.42	0.02	376	14
TS#13	F	150	21/01/12	PAT	29	1,426	118.9	2.7	480	9
TS#14	F	245	27/03/12	PAT	28	4,212	135.9	6.8	904	7
TS#15	F	250	8/04/12	SPOT	408	15791[b]	50	1.5	n/a	6
TS#16	M	288	15/04/12	SPOT	–	–	–	–	–	–
TS#17	F	210	27/04/12	SPOT	107	3,020	29.0	1.0	n/a	13.6
Total					1,007	19,505	–	–	–	–
Mean					67.13	2,715	51	2.6	539	10.69
Median					28	1,923	41.2	2.6	480	9
SD					105.57	4,116	40	1.74	263.59	4.76

Tags on sharks TS#18, TS#11 and TS#16 failed to transmit data. The UKF state-space model could not determine accurate tracks for short-term PAT deployments on TS#5 and TS#6. Due to potential error around calculated daily position estimates for PAT, mean step length and speed for these sharks are indicative only

[a] Tag recovered

[b] First 300-day deployment

13 sharks, with TS#5 and TS#6 having insufficient dawn/dusk information to allow the geolocation models to converge. Depth and temperature profiles were, however, obtained from all 15 sharks.

Days at liberty for PAT-tagged tiger sharks were between four and 58 days (mean = 20 days). Fin-mounted SPOT5s remained on fish for longer, transmitting for periods of between 103 and 408 days (mean = 190 days) (Table 1). The quality of the location classes was noticeably reduced after approximately 300 days at liberty, with several weeks lapsing between retrieval of usable LC3–1 quality data. As a result, the distance calculations for TS#15 (Table 1) were restricted to the first 300 days of deployment to reduce the potential error in overall estimates. Two of the PATs were recovered, providing 63 days of high-resolution archived data. Of the remaining nine PATs, 91 ± 4 % (mean and SD) of the transmitted data were successfully decoded. Mean daily movements ranged from 0.42 to 135.9 km day^{-1} (±40 km day^{-1}), with an average speed of 2.6 km h^{-1} (±1.74 km h^{-1}).

Season, size and sex

Fishing trips were conducted across all seasons, with most tiger shark catches occurring in NSW from spring to early autumn (11 of 13 captures). Three of five captures in QLD occurred during the winter months. Of the 18 sharks tagged, only three were males, of which only two yielded tracking data. The majority of tiger sharks tagged in this study were either juvenile or sub-adults, with possible exception of five individuals over 310 cm TL (Table 1). While the calcification state of the claspers was not noted, mating scars were not obvious on any of the females examined during tag deployment. Shark size did not influence distances travelled ($\chi^2 = 0.41$, $df = 1$, $p > 0.05$) or inshore/offshore habitat preferences. TS#7, however, did show strong site fidelity to the waters near the Noosa region (26°23′S 153°9′E) throughout its 103-day tag deployment. As a result, TS#7 had the highest percentage (28 %) of time at cooler temperatures (18.1–20.6 °C) during winter, in contrast to other sharks that moved offshore into warmer shelf waters.

Vertical habitat use: depth and temperature

Tiger sharks spent considerable time in the epipelagic zone above the thermocline in depths of less than 100 m, but were recorded diving to depths of up to 920 m. Water temperature ranged from 29.5 °C at the surface and 5.9 °C at depth (Table 1). Overall, binned depth and temperature profile data indicated that tiger sharks spent the majority of their time at shallow depths and warm temperatures. Mean proportions of time-at-depth

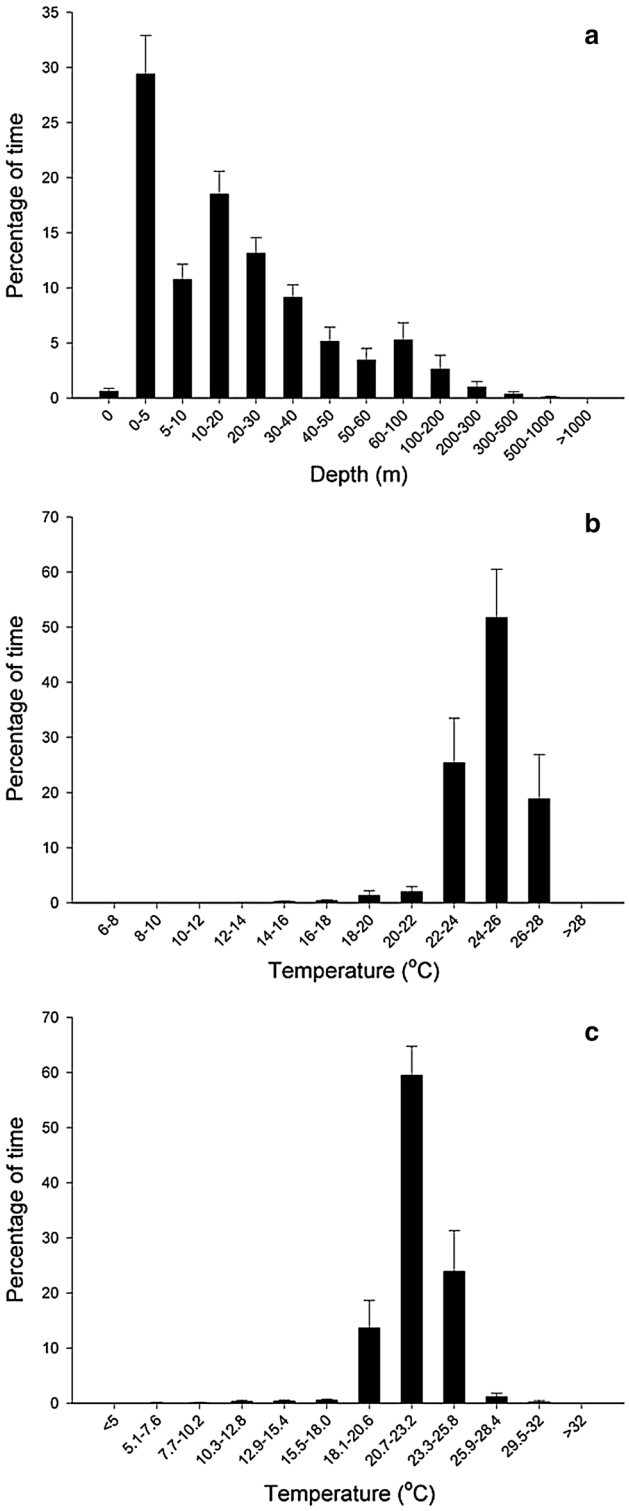

Fig. 2 Cumulative percentage of time-at-depth and time-at-temperature for PAT- (**a, b**) and SPOT5-tagged (**c**) tiger sharks

for PAT-tagged individuals ($n = 9$) revealed that 59 % of their time was spent at depths of <20 m and 87 % of their time in <50 m (Fig. 2a). The use of the upper water

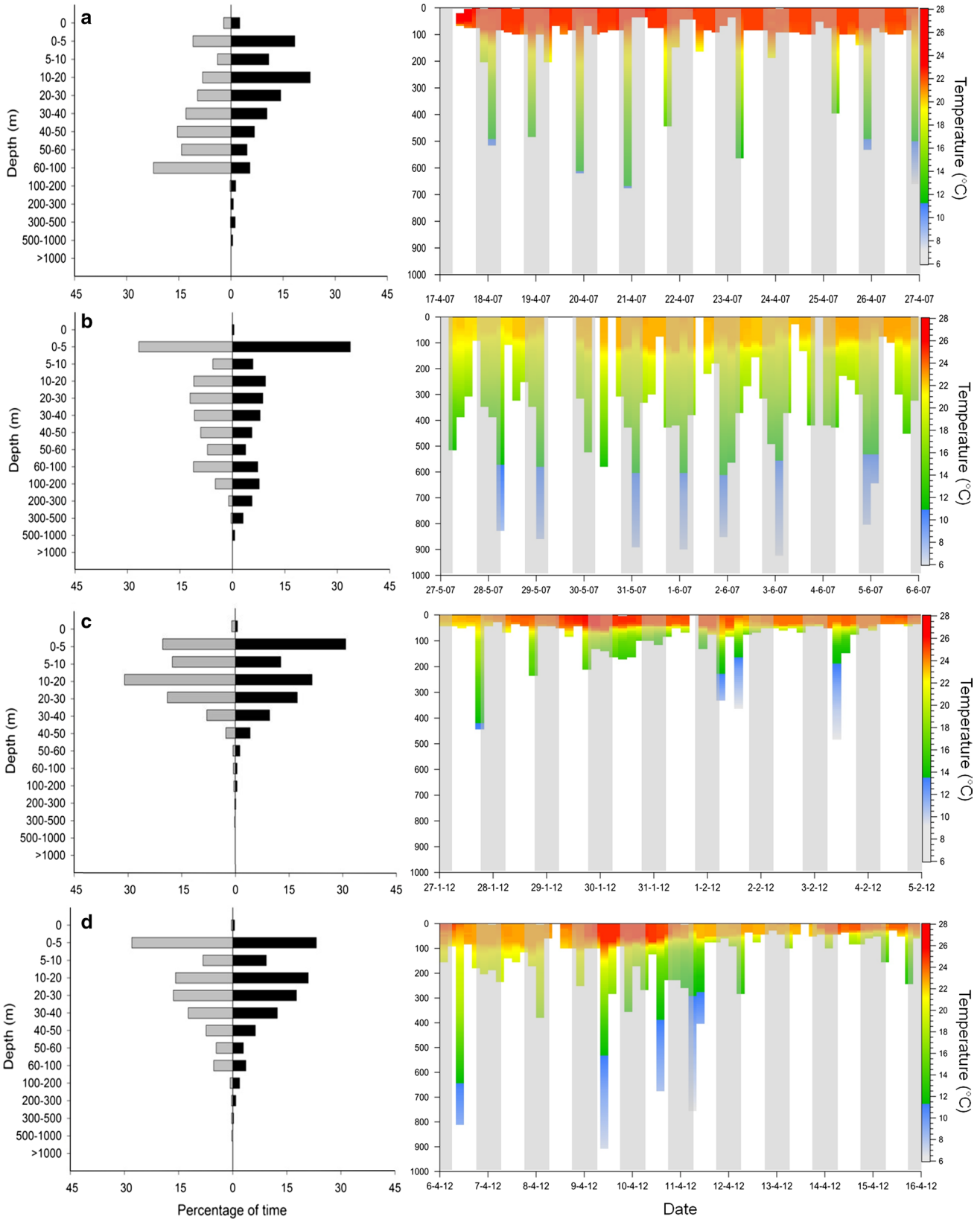

Fig. 3 Histograms of percentage time-at-depth (4-hourly binned data) for day (*grey bars*) and night (*black bars*) for duration of deployment for PAT-tagged **a** TS#1, **b** TS#2, **c** TS#13 and **d** TS#14. Associated depth-temperature graphs produced by Igor Pro show selected 11-day summary periods for each deployment. *White bars* indicate day time

column was also reflected in the water temperature profiles, with over 50 % of the deployment time spent in the 24°–26 °C temperature bin (Fig. 2b). Conversely, SPOT5-tagged individuals ($n = 4$) spent approximately 60 % of the time in the slightly cooler 20.7–23.2 °C temperature bin (Fig. 2c).

Depth profiles obtained from four-hourly binned data did not indicate any clear diel patterns, though the vertical range was broader during the night (night: 322 ± 138 m; day: 220 ± 263 m; paired t test, $t = -4.238$, $n = 128$, $p < 0.001$) (Fig. 3 for (a) TS#1, (b) #2, (c) #13, (d) #14). Analysis of the full high-resolution archived data from TS#3 indicated that deep dive (>500 m) durations were often brief. For example, the deepest return dive from the surface to 872 m occurred at 0555 h on 21/12/07 and took just 37 min to complete (Fig. 4a). Patterns of oscillatory or yo–yo diving behaviour appeared evident at shallower depths (*c*. 150–200 m). These dives were characterised by longer durations at depth (≈15 min per dive) and interspersed with regular returns to the surface over many hours (Fig. 4c). Similar dive types were also evident from recovered archived data from the shorter deployment on TS#6 (Fig. 4b, d). The FFT analysis conducted on TS#3 archival data did not identify any diel pattern in diving behaviour.

Horizontal movements and kernel density

High-quality long-term horizontal movement tracks were obtained for two small and two large (±250 cm TL) SPOT5-tagged tiger sharks (TS#7, #10, #15, #17; Fig. 1). The smallest of these individuals (TS#7) remained within 80 km of its tagging location. Two sharks (TS#15 and TS#17) were tagged in temperate NSW waters in the austral autumn and travelled north to subtropical QLD waters during the winter months (June–August). The longest tag deployment (TS#15; 408 days) then returned to NSW waters in the austral spring (October) and continued to move down the east Australian coastline throughout summer to offshore from Eden (37°4′S, 149°54′E) near the NSW/Victoria state border. By April (austral autumn), TS#15 had returned to the offshore waters adjacent to Sydney where it had been tagged at the same time the year before. TS#10 stayed predominantly in QLD waters for the duration of the tag deployment and moved to warmer (>20 °C) offshore shelf waters in the winter months. When transiting the coast, TS#10, #15 and #17 all travelled along the shelf edge, making infrequent visits to nearshore waters. The average ROM for these four sharks over the duration of their tag deployments was 14.8 ± 13 km day^{-1} (TS#7), 46 ± 61 km day^{-1} (TS#10), 50 ± 346 km day^{-1} (TS#15) and 29 ± 60 km day^{-1} (TS#17), respectively.

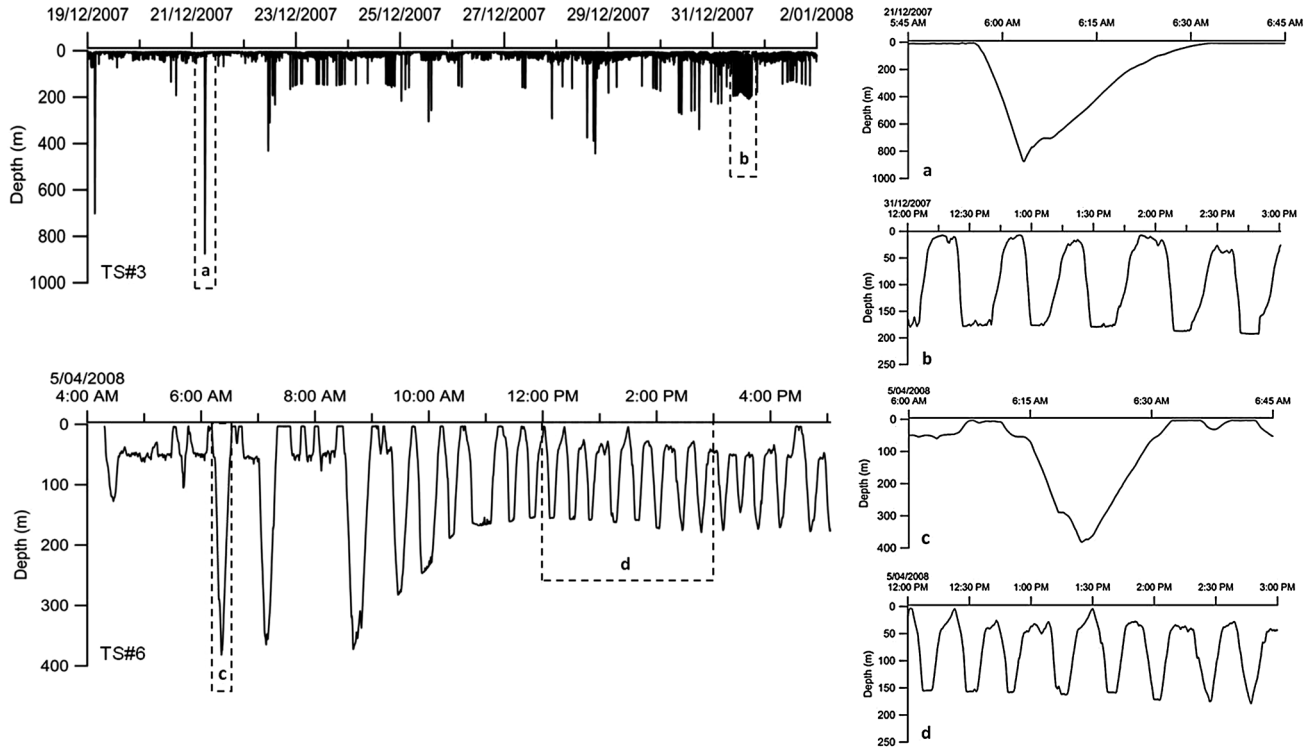

Fig. 4 Dive archive for TS#3 (sub-sampled for a 2-week period) and TS#6 (sub-sampled for a 1-day period). Secondary graphs depict brief deep diving behaviour (**a**, **c**) and yo–yo diving behaviour (**b**, **d**)

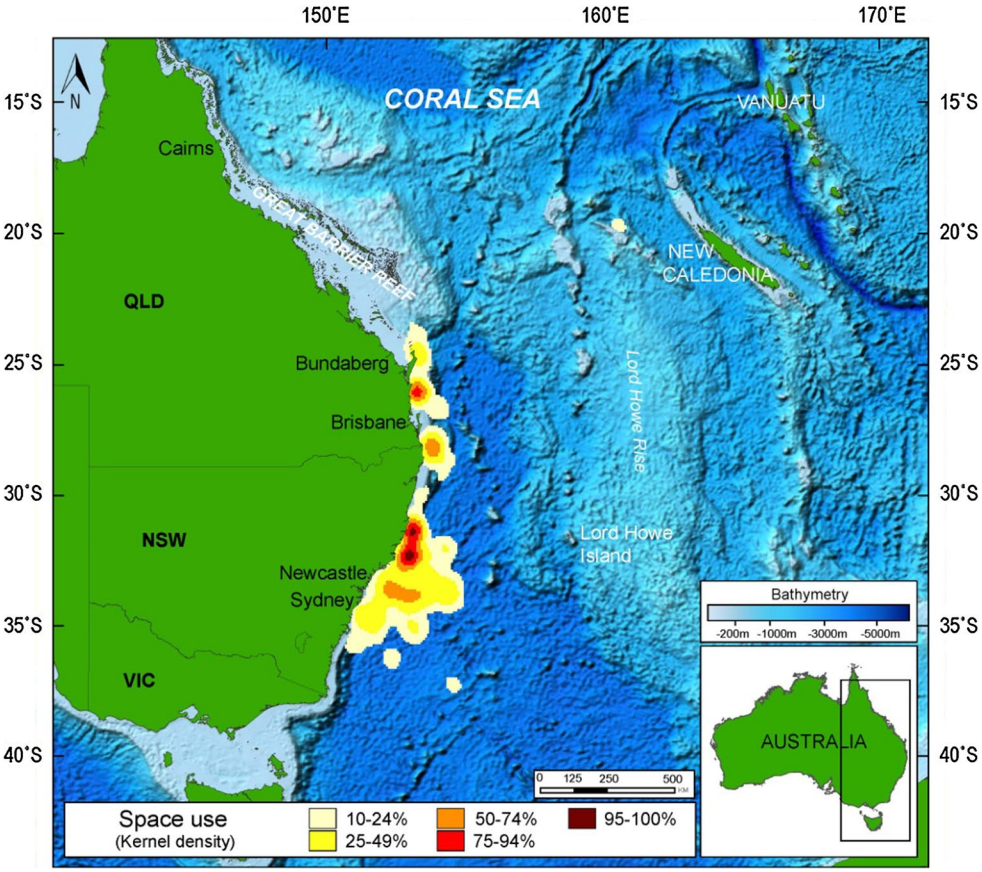

Fig. 5 Kernel density analysis showing areas of high use by *G. cuvier* off of the east coast of Australia

The UKF state-space model provided corrected movement tracks for 11 PAT-tagged sharks (Fig. 1). The majority of sharks tagged off NSW maintained a localised (*c*. 400 km) range between Port Macquarie (31°25′S, 152°54′E) and Bega (36°40′S, 149°49′E). Three sharks (TS#8, TS#13 and TS#14) moved further south past the Victorian state border to offshore Tasman Sea waters. TS#2 undertook the greatest migration (*c*. 1,800 km straight line distance) from offshore Sydney to Nereus Reef, east of the Chesterfield Islands group in New Caledonian waters. Both PAT-tagged sharks in QLD (TS#9 and TS#12) moved immediately to deeper waters after tagging, with TS#9 travelling from Noosa (26°22′S, 153°9′E) to the QLD/NSW border in 9 days.

Kernel density analysis using the daily locations of each tiger shark showed that the main areas of activity (between 95 and 100 %) for the sharks tagged in this study were off Seal Rocks (32°27′S, 152°31′E) and Port Macquarie in NSW. Other areas of high use (between 50 and 94.9 %) were identified on the Sunshine Coast between Noosa and Double Island Point (25°56′S, 153°11′E) in QLD (Fig. 5). High-use areas in NSW were predominantly confined to continental slope waters, whereas activity in QLD waters was typically in offshore continental shelf waters.

Discussion

This study represents the first to observe migratory behaviours of tiger sharks near to the southern extent of their latitudinal range in the south-western Pacific Ocean. Although the sample size was small ($n = 15$) and restricted to predominantly female sub-adults, there were several broad similarities in behaviour among individuals including wide-ranging patterns of movement and visitation to the same locations. This is consistent with studies elsewhere that have shown tiger sharks to alternate between localised and extensive movements that may encompass a variety of habitats (Holland et al. 1999; Heithaus et al. 2007; Meyer et al. 2010; Hammerschlag et al. 2012). Further, horizontal movements were similarly characterised by transient behaviour, through directional swimming of up to several hundred kilometres (Holland et al. 1999; Jorgensen et al. 2010; Meyer et al. 2010; Papastamatiou et al. 2011), coupled with smaller scale (<25 km) resident behaviour, through area restricted swimming that repeatedly cover the same areas (Meyer et al. 2009; Jorgensen et al. 2010). Seasonal pole-ward movements into waters over 40°S were also identified, which is further south than previously reported for the species in this region. Daily step lengths recorded in this study provided estimates of movement

speed for *G. cuvier*. Due to the potential statistical errors arising from the accuracy of PAT geolocation data, the geodetic distances calculated for PAT-tagged individuals are indicative only and may not be accurate. Nonetheless, the mean speed (km hour^{-1}) and mean step lengths (km day^{-1}) observed were similar to those reported in other tiger shark tagging studies elsewhere (Holland et al. 1999; Stevens et al. 2000; Kohler and Turner 2001).

In this study, movement paths on the Australian east coast were most often associated with the 200 m shelf-edge isobath or mid-continental shelf areas, with infrequent visits to nearshore waters. Bathymetric features such as the shelf-edge isobath or underwater seamounts may serve as navigational aids, particularly during broad-scale movements (Klimley 1993; Litvinov 2007). This was evident during the migration of TS#2, which after leaving the Australian EEZ travelled along the Lord Howe Rise, a deep-sea marginal plateau surmounted by small volcanic islands and seamounts that is influenced by eddies shed from the EAC (Harris et al. 2012). Ocean currents may also influence tiger shark movements (Hazin et al. 2013), and the seasonal fluctuations in the strength of the southward-flowing EAC likely contribute to the time spent in offshore waters in this region. Indeed, the unique oceanography parallel to the Australian coast between 32° and 39°S is known as 'Eddy Avenue', an area commonly containing large anticyclonic eddies causing sea surface temperature anomalies in the region. Smaller cyclonic eddies are also common and promote higher chlorophyll *a* levels (Everett et al. 2012). Warmer temperatures and higher levels of primary productivity may explain the use of these habitats by tiger sharks, particularly during the austral summer.

Latitudinal range extension during the summer months was realised through long-term (>100 day) deployments of SPOT5 tags. Retraction from temperate NSW waters into subtropical QLD waters occurred when water temperatures dropped below 19 °C (July–September) and when the southward-flowing EAC is at its weakest (Ridgway and Godfrey 1997). Interestingly, both sharks that were SPOT5-tagged in NSW undertook very similar travel paths north into QLD waters at the same time of year. These movements, coupled with reduced commercial and recreational catches of sharks in NSW in the winter months, indicate that perhaps year-round residency at latitudinal extremes (>30°S) for this species is rare. Indeed, targeting behaviour of shark game fishers in NSW shifts to short fin mako (*Isurus oxyrinchus*) in the colder months due to the scarcity of tiger sharks (Stevens 1984; Pepperell 2008). Further, due to historically low catches of 'dangerous' sharks in winter, including tiger sharks, since 1982 the NSW Shark Meshing Program has routinely removed shark nets from beaches in the May–August period each year to mitigate against whale entanglements (Green et al. 2009). Although latitudinally lower than NSW, Heithaus (2001) also reported a significant reduction in winter catch rates of tiger sharks when water temperatures dropped below 20 °C in Shark Bay, Western Australia (25°45′S, 113°44′E). Of the two long-term SPOT5s deployed in QLD, both individuals remained in the subtropics into late spring when other tagged sharks were observed returning to NSW. This residency behaviour is supported by year-round commercial fishing and QLD shark control captures of tiger shark in southern QLD (DEEDI, unpublished data; Holmes et al. 2012), indicating that individual decisions to move within warmer subtropical waters may not be influenced by extrinsic temperature factors alone. Indeed, Papastamatiou et al. (2013) found that variations in warmer water temperatures (23–26 °C), coupled with chlorophyll *a* concentrations, were probably proxies for marine productivity, thus influencing tiger shark utilisation of other areas.

Despite a seemingly clear correlation with water temperature, there are other extrinsic factors that may influence shark movements, such as prey availability. Such factors are harder to identify, although annual, seasonal movement of tiger sharks to particular foraging areas has been documented (Lowe et al. 1996; Fitzpatrick et al. 2012). Indeed, the stronger EAC currents flowing southward during the warmer months mark a seasonal biome shift in this region, which influences the distribution of pelagic fishes such as tunas, kingfish, mackerels and billfishes (Kailola et al. 1993; Gillanders et al. 2001; Lowry and Murphy 2003; Zischke et al. 2012), as well as spawning activity by deep-sea fishes on seamounts (Rowling et al. 2010). Offshore movements of tiger sharks in Hawaii have also been linked to patterns in oceanic productivity (Meyer et al. 2010). Seasonal habitat use is likely employed by tiger sharks as an important feeding strategy as it can facilitate the exploitation of different prey arenas, reduces competition among conspecifics and may afford them a level of surprise on unwary prey (Papastamatiou et al. 2006; Meyer et al. 2009).

Given the maturity state of the individuals in this study, it is unlikely that the use of the southern sites by these sharks was due either to mating or parturition. Consideration of other intrinsic states (i.e. age and sex) on the collective movement of tiger sharks was difficult due to the limited number of long-term tagged animals of both sexes. The strong site fidelity to inshore habitat exhibited by TS#7, a 180-cm TL male, was markedly different from other small female tiger sharks tagged offshore in this study (e.g. TS#8, TS#13) which exhibited much wider-ranging movements. Although the ability for juveniles to undertake wide-ranging movements has been documented elsewhere (Meyer et al. 2009; Papastamatiou et al. 2013), intraspecific differences in habitat use may also be a behavioural feature of tiger sharks (Vaudo et al. 2014). Meyer et al. (2010) surmised that different patterns of behaviour may result from

unique, individual learning experiences, such as learning to exploit a particular prey patch. This might serve as a mechanism for intraspecific resource partitioning and may give rise to prey specialisation among individuals. Vertical habitat use of surface and deep waters (>500 m) was a ubiquitous trait exhibited by all sharks regardless of size. While tiger sharks in this region made occasional excursions below the thermocline (>100 m), the majority of time (72 %) was spent in the upper mixed layer between 0 and 30 m. Frequent use of the upper 5 m of the water column (29 %) was consistent with other tiger sharks from the north-west Atlantic (Vaudo et al. 2014), but was surprisingly in contrast to other *G. cuvier* tagged off of northern Australia and Hawaii, which spent the majority of the time-at-depths around 50–100 m. Minimum temperatures recorded during deep diving excursions of around 6–7 °C in this study were unexpected given the species' tropical classification. In addition to their deep diving behaviour, occasional residence in cooler nearshore waters in winter and movements south into temperate waters indicate that tiger sharks are clearly capable of occupying cooler water masses for reasonable periods, but still spend the majority of their time at the highest water temperature 'available' during their migrations (Brill et al. 1993).

Analysis of the full archived dive data from TS#3 and TS#6 revealed complex vertical use of the water column. Brief deep dives to over 500 m were made throughout the tag deployments and typically occurred around dawn and dusk. These dives were often characterised by rapid, almost vertical descents to well below the mixed layer followed by more gradual ascents to the surface, which is consistent with the powered swimming performed by tiger sharks in Hawaii (Nakamura et al. 2011). By contrast, continual shallower dives to around the thermocline (150–200 m) over several hours were also observed, with periods of up to 15 min spent at depth before returning to the surface. Previous studies have collectively coined these vertical movements as oscillatory or 'yo–yo' dives and attributed them to a range of potential behaviours, including thermoregulation, swimming efficiency, foraging and navigation (Carey and Scharold 1990; Holland et al. 1999; Klimley et al. 2002; Heithaus et al. 2002; Weng et al. 2007; Nakamura et al. 2011; Vaudo et al. 2014). The distinctive differences between singular 'deep' diving and concurrent 'oscillating' dive behaviour identified in this study may be indicative of two discrete diving behaviours in tiger sharks. Holland et al. (1999) postulated that brief deep dives of tiger sharks in Hawaii served as a mechanism of orientation between shallow banks. Indeed, the most consistent deep diving behaviour observed in the present study was undertaken by migrating TS#2, which correlated directly with the time of its directional swimming along the Lord Howe Rise strongly suggesting that it may have been using the plateau topography as a navigational aid. Although data were binned for this animal, the recovered tags from TS#3 and TS#6 revealed that all dives below the thermocline were brief, with total excursions not exceeding $\approx$ 30 min. Deep orientation diving to the platform edge has also been identified in north-west Atlantic tiger sharks (Vaudo et al. 2014), indicating that this behaviour is probably ubiquitous across the species. Oscillating or 'yo–yo' dive behaviours were characterised by a sequence of shallower dives followed by regular returns to surface waters over several hours. Based on location data for TS#3, dives to 150–200 m were not associated with the continental shelf edge. More likely, these dives are undertaken to the edge of the deep thermocline created by the summer flow of the EAC along this coastline (Steinberg 2007). Other studies focusing on tiger shark dive behaviours using data loggers and high-rate data recording tags also found that depth distributions did not appear to be related to horizontal movements, thermoregulation, sex or size factors and that yo–yo diving might be an optimal search strategy to detect prey (Nakamura et al. 2011; Vaudo et al. 2014). As such, we suggest that the yo–yo diving observed here is also consistent with prey searching behaviour, whereby olfactory cues that disperse along the horizontal layers may be encountered with the highest probability (Klimley et al. 2002; Weng et al. 2007). Concomitantly, tiger sharks appear to rely on stealth as a foraging tactic and using the water column vertically in this way allows them to attack prey from below, reducing the number of escapes routes particularly for near surface-dwelling prey (Heithaus et al. 2002). A diet study by Chan (2001) revealed that the major taxonomic group found in the stomachs of tiger sharks in NSW was shearwaters (*Puffinus* spp.) (41.9 %), with a high proportion also consisting of cetaceans (19.4 %). Selection for these prey in temperate waters when other favoured warm-water species are not available (i.e. marine turtles, sea snakes; Simpfendorfer 1992) likely influences the diving and hunting strategies employed by tiger sharks in this region.

By deploying satellite tags on tiger sharks to identify patterns of habitat use and the environmental determinants of movement and migration, it is immediately apparent that they are tolerant of a range of environments while also able to actively respond to environmental dynamics and disperse into new habitats. This was evident from the residency behaviour interspersed with the highly directional transient movements observed in this study. Coupled with the vertical habitat use data, tiger sharks in this region clearly undertake migrations from subtropical QLD to exploit the seasonally warm and prey abundant waters of NSW. There was no evidence of year-round residency in these southern waters, perhaps indicating that contrary to the partial migration observed in subtropical waters, 'complete' migration may occur at the latitudinal extent for this

species. While we acknowledge that the small sample size of this study may not have identified winter residents in NSW, we demonstrate that inter-annual variability in local abundances is considerable. Further, considering the inter-individual variation in both horizontal and vertical movements, it is likely that tiger sharks are incidental in their exposure to most fisheries and only as subset of the population will be vulnerable to local fisheries at a given time (Vaudo et al. 2014). As such, care should be taken when interpreting catch rate information as an indicator of population abundance of highly mobile marine animals, particularly at their latitudinal extent. With the identification of broad-scale migration occurring across the Coral Sea, local conservation initiatives alone may not be adequate in reducing the threats facing migratory sharks in this region. Our findings further emphasise the need to address marine conservation issues at both a local and an international scale.

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CHAPTER 4: AGE AND GROWTH OF THE TIGER SHARK (*GALEOCERDO CUVIER*) OFF THE EAST COAST OF AUSTRALIA

4.1 ABSTRACT

Lengths-at-age and growth rates for southwest Pacific *Galeocerdo cuvier* were estimated from vertebral growth band counts of 202 sagitally-sectioned centra from 112 females (71 – 430 cm total length (L_T)), 79 males (72 – 351 cm L_T), and 11 sex unknown. Data from measurements of growth in captivity were also examined to complement vertebral age estimations. The sexes combined modelled growth coefficient (k = 0.08) was smaller than previously reported for *G. cuvier* populations elsewhere. Split-band and narrow banding patterns were identified as potential sources of age underestimation in this species.

4.2 INTRODUCTION

The tiger shark *Galeocerdo cuvier* (Péron & Lesueur 1822) is the largest species in the family Carcharhinidae, growing to around 550 cm total length (L_T) (Holmes et al., 2012; Meyer et al., 2014). In the southwest Pacific Ocean individual sharks exhibit a range of patterns of habitat use from year-round local site fidelity, to wide-ranging ocean migrations in tropical and warm temperate waters (Fitzpatrick et al., 2012; Holmes et al., 2014; Werry et al., 2014). Off the east coast continent of Australia *G. cuvier* are caught by the commercial, recreational and game fishing sectors, and a substantial number are also caught each year through shark control programs in place on popular Queensland (QLD) and New South Wales (NSW) beaches (Fisheries, 2006; Reid et al., 2011; Holmes et al., 2012). Illegal foreign fishing activity in Australian Commonwealth waters also harvests an unquantifiable number of *G. cuvier* from Australian waters each year (Griffiths et al., 2008; Marshall, 2011). Recent research using data from game fishing activities and long term shark control programs has identified declining catch rates for *G. cuvier* on the east coast of Australia (Park, 2009; Reid et al., 2011; Holmes et al., 2012). To adequately understand the implications of these findings, examination of life history parameters is crucial to determine the extent the species' population would be affected by fishing and the ability to recover if stocks become depleted (Branstetter, 1990; Smith et al., 1998). Baseline biological information for *G. cuvier* in the southwest Pacific region, however, remains scant. The large size, semi-solitary nature and the

wide-ranging movements of this species have thus far hindered a comprehensive study of its biology, which is essential for the development of appropriate management strategies. Knowledge of length-at-maturity, maximum age and growth rate are pre-requisites for any age-based methods of stock assessment (Wintner and Dudley, 2000).

Elasmobranch age determination typically utilises the concentric pairs of wide opaque and narrower translucent bands found in the vertebral centra (Cailliet and Goldman, 2004). Although *G. cuvier* have a global distribution in tropical and warm temperate waters, vertebral ageing studies of the species using this method have only been conducted in Hawaii (n = 28 individuals; De Crosta et al., 1984); western North Atlantic (n = 238; Kneebone et al., 2008), Gulf of Mexico (n = 69; Branstetter et al., 1987), and off the east coast of South Africa (n = 101; Wintner and Dudley, 2000). Moreover, back-calculation methods were often used as full size ranges for the species were not able to be obtained. *G. cuvier* growth has also been assessed through the use of mark-recapture methods in Hawaii (n = 37, Meyer et al., 2014), western North Atlantic (n = 42; Natanson et al., 1999; n = 217; Kneebone et al., 2008), and off Brazil (n = 2; Afonso et al., 2012). Small samples sizes, low rates of recapture and a lack of representation of the species' full size range are generally limiting features of such studies (Meyer et al., 2014). Irrespective of the method used, however, modelled estimates of the growth coefficient, k, and asymptotic total length, L_∞, appear to be markedly different for *G. cuvier* in different regions of the world.

Previous studies have demonstrated that centrum banding patterns in elasmobranchs may be related to physiological changes induced by changes in environmental parameters such as temperature and photoperiod (Cailliet et al., 1986; Goldman, 2005), and evidence of subtle banding due to food shortages has been suggested in some species (Goldman, 2005). Regional differences in prey availability may also affect growth rates (Wirsing et al., 2006), highlighting the need for regional assessments to be completed. Indeed the movement capabilities of *G. cuvier*, particularly across the southwest Pacific, are seasonal and wide ranging, and encompass the use of both tropical and warm temperate waters, thus encountering a wide variety of locally-abundant prey species throughout their distribution (Holmes et al., 2014; Werry et al., 2014). The aim of the present study was to examine the age and growth of *G. cuvier* off the east coast of Australia using vertebral band-pair

counts from pre- and post-natal individuals. Growth rates were able to be compared with length-mass data from captive reared *G. cuvier* at SeaWorld, Gold Coast. Assessment of mark-recapture *G. cuvier* data collected by citizen scientists through the NSW Game Fish Tagging Program (NSWGFTP) was also conducted. In addition to providing the first growth model and length and age at maturity estimates for *G. cuvier* in the western Pacific, we also identify and discuss pre-birth banding and split banding patterns for the first time in *G. cuvier*.

4.3 MATERIALS AND METHODS

4.3.1 Sample Collection

Queensland

G. cuvier vertebrae were collected from individuals caught in the Queensland Shark Control Program (QSCP) between 2008 and 2011, with the geographic range of collection from Cairns in tropical northern QLD (16°55´S 145°46´E) to the sub-tropical Gold Coast region (28°10´S 153°33´E) near the NSW border (Figure 4.1).

New South Wales

Vertebrae were collected along the NSW coast between Coffs Harbour (30°18´S 153°7´E) and Bermagui (36°2´S 150°4´E) from *G. cuvier* caught as part of recreational game fishing operations between 1997 and 2000. These samples were complemented by vertebrae collected by the NSW Fisheries Observer Program (NSWFOP), which conducted fishery-dependent sampling of commercially caught sharks north of Crowdy Head (31°50´S 152° 45´E) from September 2007 to July 2009. Additional vertebrae were provided from the NSW Shark Meshing Program (NSWSMP) captures between Bondi (33° 53´S 151° 15´E) and Wattamolla (34° 8´S 152° 7´E) from 2004 to 2006 (Figure 4.1).

4.3.2 Processing of animals

For most samples, capture date and location, total length (L_T) (±1 cm) and sex were recorded. Total length was determined by allowing the caudal fin to take a natural position, with measurements taken underneath the animal in a straight line.

For whole sharks obtained from the QSCP, fork length (L_F) and pre caudal length (L_{PC}) (±1 cm) were also recorded. For NSW gamefishing samples, L_T was provided for all samples, with L_F and L_{PC} provided for a subset of samples. Where L_F or L_{PC} was not recorded, the values were calculated using a length-length conversion calculated by the regression relationships among L_T, L_F and L_{PC} from the sampled population using SigmaPlot 11.0 (Systat Software Inc. Chicago, IL). A chi-square goodness-of-fit test was conducted to examine whether the sample was sex-biased (PASW Statistics V.18) at four life stages; pre-natal, juvenile (birth – 200 cm L_T), sub-adult (200 cm L_T – 300 cm L_T) and adult (300 cm L_T +). Sex ratio by fishing method was also assessed. A Shapiro-Wilk test for normality was conducted to determine whether the size frequency distribution of either sex was skewed. Up to 10 vertebral centra were removed from the cervical region from all sharks, where vertebrae are largest in diameter, facilitating more accurate age estimates than vertebrae from other regions (Officer et al., 1996). Vertebral samples from *in utero* pups from three different litters were also processed to examine the presence of pre-birth banding. These pre-natal samples consisted of pups near full term growth (>71 cm L_T) and were therefore included in the growth modelling analyses for comparison with post-natal only data, and potential to assist in anchoring the lower end of the growth curve (see Silva et al., 1996; White et al., 2001; White et al., 2002).

Where possible reproductive state was determined from the maximum oocyte diameter (MOD), ovary and oviducal gland mass of females; and from clasper length and calcification state for males (Walker, 2005; Whitney and Crow, 2007). The length and age at which 50% of the population was mature (L_{50} and $A_{50,}$ respectively) were determined for each sex using 50 cm L_T size classes and 2-year age classes. A least-squares non-linear regression (PASW Statistics V.18) using the logistic function

$$P(l) = 1 \cdot \left(1 - e^{-\ln(19)\left(\frac{l - L_{50}}{L_{95} - L_{50}}\right)}\right)^{-1}$$

(Walker, 2005)

enabled calculation of parameter estimates. $P(l)$ is the proportion of mature animals at L_T l, and the lengths at which 50% and 95% of the population is mature are represented by L_{50} and L_{95}, respectively. For A_{50}, the proportion of mature animals in

each age class (a) was substituted for l, with L_{50} and L_{95} replaced by A_{50} and A_{95}, respectively (Gutteridge et al., 2013).

4.3.3 Captive sharks

Between June 2003 and September 2006, three *G. cuvier* were maintained for 239, 425 and 1031 days in outdoor aquaria at SeaWorld, Gold Coast. Data on mass (kg) and L_T (±1 cm) were recorded at the time of capture and again at release. Mean growth rate was calculated for each specimen by dividing the total observed growth by their time in captivity.

4.3.4 Mark-recapture

As part of the NSWGFTP, 26 *G. cuvier* were tagged and recaptured between 1985 and 2014, and capture/recapture dates, L_T or L_F (m) and mass (kg) when captured/recaptured were recorded by recreational fishers. As indicated on tagging program data sheets, initial capture data were always estimated *in situ*, and recapture data were either estimated or directly measured if the shark was killed and weighed at the wharf. Data were assessed for reliability, and found to be highly inconsistent and deemed unusable for length and/or mass estimates, and were subsequently discarded from the analyses.

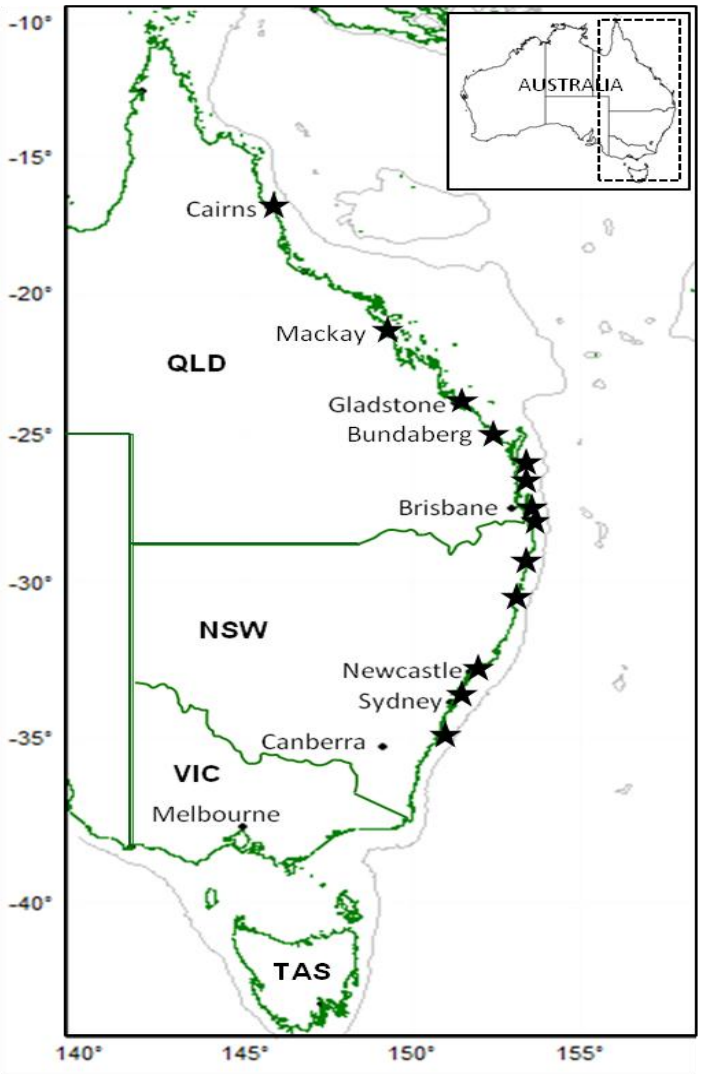

Figure 4.1: Map of study area on the east coast of Australia. Black stars indicate where vertebral samples were collected from locally caught *G. cuvier*.

4.3.5 Vertebrae preparation and ageing protocol

All vertebral samples collected from dissected individuals were stored frozen until processing. Individual centra were cleaned of soft tissue, and the neural and haemal arches removed. For larger specimens, submersion in a 10% sodium hypochlorite solution for up to 60 minutes, followed by washing in distilled water, aided excess tissue removal. Cleaned centra were stored in 70% ethanol (Wintner and Cliff, 1996). For each *G. cuvier*, one vertebra was chosen at random for sectioning. Small vertebrae (< 1 cm diameter) were embedded in a clear polyester resin (Diggers, Reochem, Brisbane) to facilitate sectioning. For each vertebral sample, a sagittal-plane 150 µm thick section was taken through the focus of the centrum with a LECO 801–137 diamond wafering blade (Buelher Isomet Low Speed saw). This thickness was chosen after conducting readability trials also using 300 µm, 450 µm and 600 µm sections (Gutteridge et al., 2013). Following sectioning, samples were polished with P400 grit wet emery paper for optimum resolution. Centra cross-sections were then set on glass slides using Polyplex Clear Cast 20 waxed resin (Fibre Glass International) and dried overnight. Experimentation with crystal violet and silver nitrate stains was undertaken to compare with unstained vertebral band counts to determine the best preparation method (Goldman, 2005). Neither of these methods produced a marked increase in band resolution, however, hence band counts were determined using natural, unstained sections.

Individual sections were viewed using transmitted and reflected light sources, with the best resolution achieved using reflected light on a dark background. A dissecting microscope (Olympus SZ) fitted with a digital camera allowed photographing and reviewing of sections using ImageJ software (http://rsb.info.nih.gov/ij/). Most vertebral sections displayed a pattern of alternating opaque and translucent zones that consisted of both narrow and widely spaced concentric ‘rings’. Following Cailliet et al. (1983), each opaque and translucent pair was defined as a growth ‘band’. Age counts were assigned to vertebral sections by marking individual band-pairs on the digital images along the line of the corpus calcareum from the birth band to the outer edge (Figure 4.2). The birth band was identified where an angle change on the centrum was apparent (Goldman, 2005). The consistent location of this band was confirmed through comparison of the birth band radius measurement to the centrum radius of full term pre-natal and young-of-the-year

(YOY) *G. cuvier*. Centrum radius (mm) and L_T (cm) were compared to examine linear relationships in growth. The readability of each vertebral section was given a score (1 – 5) according to the following definitions derived from Geraghty et al. (2014): (1) all growth-bands well defined and visible; (2) almost all bands visible, clear interpretation possible; (3) most bands visible, interpretation reliable to within ± 1; (4) bands visible, majority difficult to interpret; and (5) unreadable. All sections deemed to be of readability 5 were excluded from further analyses. Two training counts were performed on all centra in the first instance (Pierce and Bennett, 2009; Gutteridge et al., 2013). Ages were then estimated from three independent counts conducted by both the primary author (B. Holmes, Reader 1) and secondary author (V. Peddemors, Reader 2) without prior knowledge of the size, sex or date of capture for each shark. Age counts that were in agreement between readers from the third independent read were adopted as the final age count for those vertebral sections. Where agreement was not reached, the archived images of each reader's ageing interpretations were reviewed and recounted in the presence of both readers (Goldman, 2005; Piercy et al., 2007). If consensus could not be reached, the sample was discarded from the analysis. Lastly, age estimates were assessed for precision and bias between readers. The precision between the final counts of both readers was tested by percentage agreement (PA; Goldman, 2005; Cailliet et al., 2006), the coefficient of variation (CV; Chang, 1982) and the average percentage error (APE; Beamish and Fournier, 1981). An age-bias plot was also constructed to test for bias between the third counts of the two readers (Cailliet et al., 2006).

4.3.6 Data analysis

Evidence of annual band-pair deposition (up to 20 years) has been validated for *G. cuvier* in the northwest Atlantic using bomb-radiocarbon techniques (Kneebone et al., 2008). Partial verification has also been obtained through marginal increment analysis in the northwest Atlantic (Branstetter et al., 1987) and the Indian Ocean (Wintner and Dudley, 2000). Due to the extremely low number of mark-recaptures of *G. cuvier* off the east coast of Australia (~2.4%; NSW DPI, unpubl. data), marginal increment analysis was conducted to qualitatively verify the timing of band deposition by observing the translucency or opacity of the centrum edge (Cailliet and Goldman, 2004). Only sections from post-natal individuals displaying clearly defined growth

bands on the centrum outer margin were included (readability 1–3; *n* = 142). Marginal increment ratios (MIR) were then calculated using the following equation, with means subsequently plotted by month of capture (± S.D.);

$$\text{MIR} = {}^{\text{MW}}/_{\text{PBW}}$$

(Conrath et al., 2002)

where MIR = marginal increment ratio; MW = margin width; and PBW = previous band pair width. A one-way ANOVA and Tukey post-hoc test was conducted to observe significant differences between mean monthly MIR.

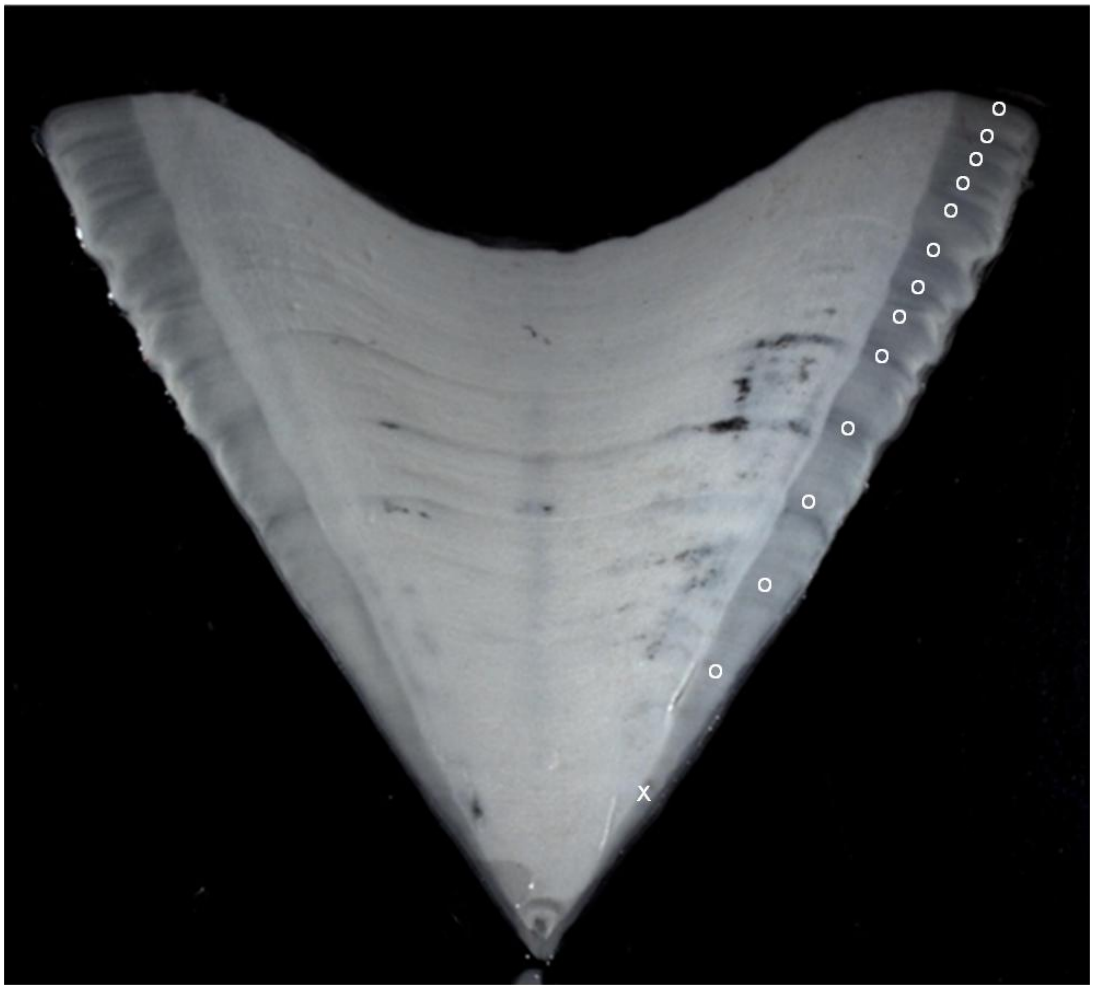

Figure 4.2: Marked vertebral section from a 285 cm TL female *G. cuvier*, with 13 growth-band pairs visible. White cross in the corpus calcareum denotes the birth band.

4.3.7 Growth modelling

Growth studies on elasmobranchs, including *G. cuvier*, have typically been modelled using the von Bertalanffy growth function (von Bertalanffy, 1938). Studies in recent years using a multiple model approach have, however, established that alternative models may be more appropriate in some shark species (Natanson et al., 2006; Barreto et al., 2011; Geraghty et al., 2014). Therefore an information-theoretic, multi-model inference (MMI) approach was used (Burnham and Anderson, 2001; Harry et al., 2013) to determine the most appropriate growth model for *G. cuvier* in eastern Australian waters. Six candidate models were fitted to observed length-at-age data for both post-natal and pre- and post-natal data sets, using modified 3-parameter versions of the von Bertalanffy (VB3), Gompertz (GOM3) and logistic (LOGI3) growth models as per Geraghty et al. (2014), where L is a function of time t, L_∞ is the theoretical asymptotic length, L_0 is length at birth and k is the growth coefficient:

Model	Equation
VB3	$L_t = L_0 + (L_\infty - L_0)\left(1 - e^{(-kt)}\right)$
GOM3	$L_t = L_0 \left(e^{\ln\left(\frac{L_\infty}{L_0}\right)\left(1-e^{(-kt)}\right)}\right)$
LOGI3	$L_t = \frac{L_\infty . L_0 . e^{(kt)}}{L_\infty + L_0\left(e^{(kt)}-1\right)}$

Two-parameter versions of the same models were also computed by substituting L_0 for a fixed length at birth taken from the largest near-term embryo observed in the present study (L_T = 78 cm). All models were fitted using least-squares non-linear regression in the statistical package R (R Development Core Team, 2014). To test for significant differences between the growth curves of females and males, VB3 results were tested for equality using a log-likelihood ratio test (Kimura, 1980). Model performance was evaluated using Akaike's Information Criterion (AIC), with the best fit model displaying the lowest AIC value (Burnham and Anderson, 2002). AIC differences (Δ) were calculated and used to rank the support of the remaining models relative to the statistical best-fit model; models with Δ = 0–2 had substantial support, Δ = 4–7 moderate support, and $\Delta \geq 10$ minimal support (Burnham and Anderson, 2002). Akaike weights (ω) were then calculated to determine the weight of evidence in favour of a particular model being the best fit to the data (Burnham and Anderson,

2002). The 95% confidence intervals (CI) around the best-fit parameter estimates were calculated from 10,000 re-sampled datasets.

4.4 RESULTS

4.4.1 Samples collected

Vertebrae from 180 post-natal (92 – 430 cm L_T) and 59 pre-natal *G. cuvier* (41 – 78 cm L_T) were collected, totalling 239 individuals of which 138 were female, 90 were male, and 11 were of unknown sex. Both female and male size frequency distributions did not conform to normality (♀: $W = 0.90$, $n = 138$, $P < 0.05$; ♂: $W = 0.94$, $n = 90$, $P < 0.05$) (Figure 4.3). Chi-squared analysis of the pre-natal, juvenile, sub-adult and adult life stages revealed that the female to male sex ratio of only the pre-natal sharks was significantly different (1.8:1, $\chi^2 = 4.34$, d.f. = 1, $p = < 0.05$). Female to male sex ratios were not significantly different for *G. cuvier* captured either by offshore gamefishing (1:1.2) or commercial operations (1.04:1); however, significantly more females than males (2.3:1) were captured on shark control gear ($\chi^2 = 12.66$, d.f. = 1, $p = < 0.05$). A linear relationship was found between centrum radius (mm) and shark total length (cm) (Figure 4.4). Relationships among L_T, L_F, L_{PC} and M were represented by the following equations:

$$L_T \text{ (cm)} = 22.607 + (1.096 * L_F \text{ (cm)}) \ (R^2 = 0.99, p = < 0.05)$$

$$L_F \text{ (cm)} = -18.812 + (0.903 * L_T \text{ (cm)}) \ (R^2 = 0.99, p = < 0.05)$$

$$L_{PC} \text{ (cm)} = -16.219 + (0.795 * L_T \text{ (cm)}) \ (R^2 = 0.92, p = < 0.05)$$

$$L_T \text{ (cm)} = 34.321 + (1.159 * L_{PC} \text{ (cm)}) \ (R^2 = 0.92, p = < 0.05)$$

$$M_b \text{ (kg)} = 1.42.10^{-7} \ (L_T \text{ (cm)})^{3.669 \pm 0.063} \ (R^2 = 0.98, p = < 0.05)$$

$$M_b \text{ (kg)} = 2.748.10^{-6} \ (L_F \text{ (cm)})^{3.245 \pm 0.042} \ (R^2 = 0.99, p = < 0.05)$$

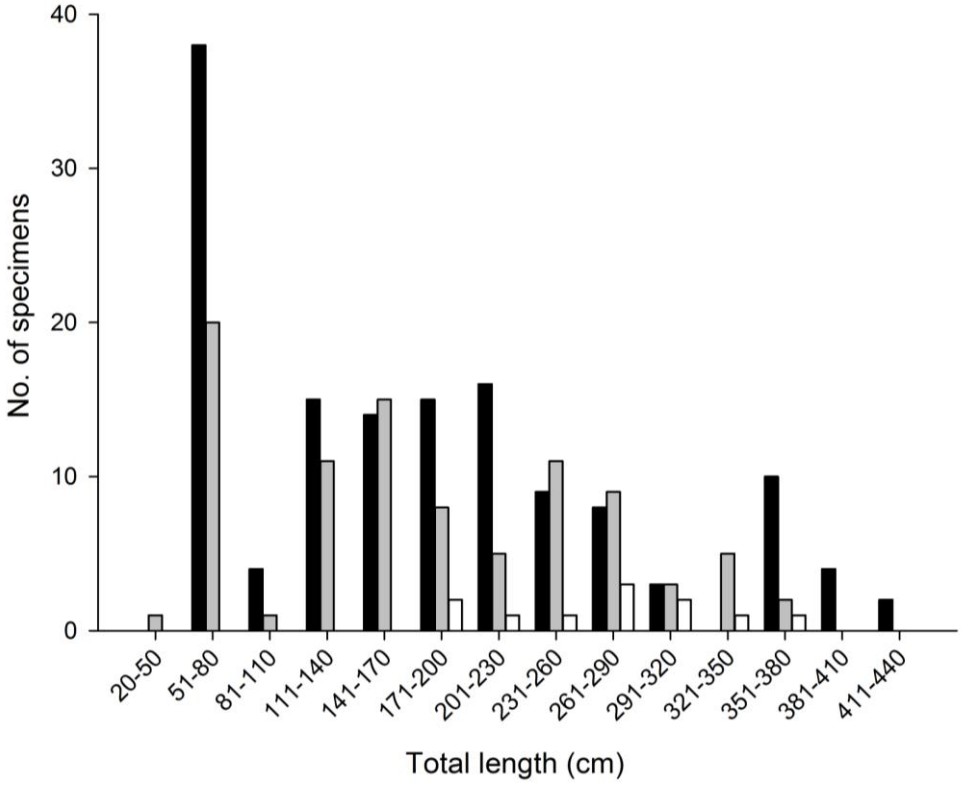

Figure 4.3: Length-frequency distributions of female (black; *n* = 123), male (grey; *n* = 91) and unsexed (white; *n* = 11) *G. cuvier* sampled from the east coast of Australia.

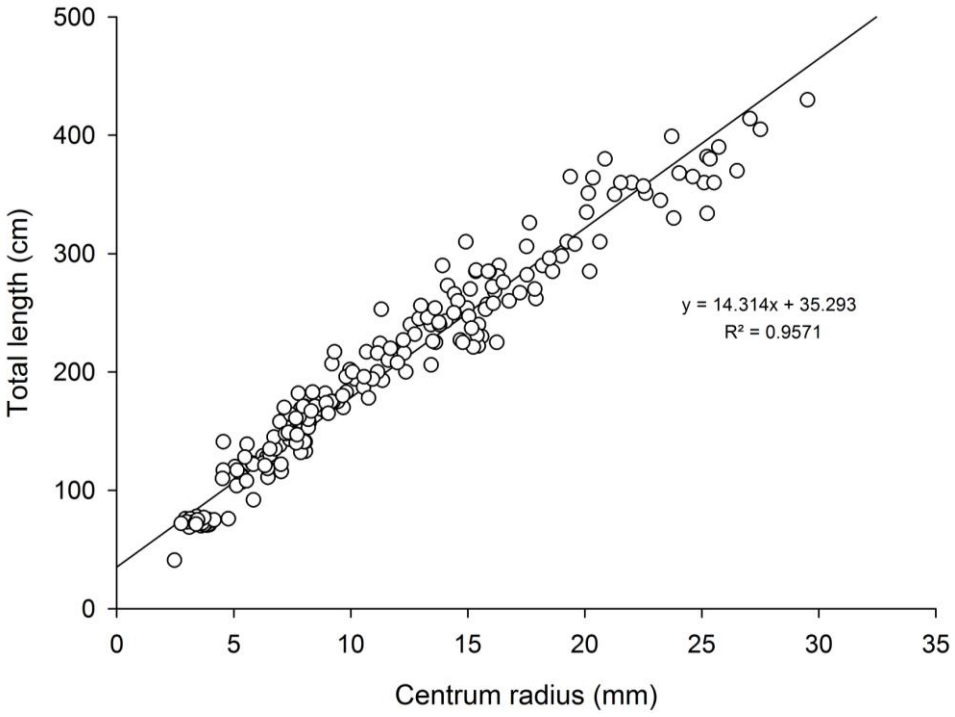

Figure 4.4: Relationship between centrum radii (mm) and total length (cm) for *G. cuvier* on the east coast of Australia.

4.4.2 Age validation

Marginal increment analysis provided evidence for annual band-pair deposition in *G. cuvier* off the east coast of Australia. Formation of the translucent narrow band (annuli) was observed in the austral winter (June – August) when MIR were lowest, with full band-pair deposition correlating with the maximum values observed in the austral spring/summer months (September – February; Figure 4.5). One-way ANOVA was significant (p = 0.005), with a Tukey post-hoc test indicating that the January mean was significantly different from April, June and August means ($p < 0.05$).

4.4.3 Pre-birth marks

Pre-birth marks were observed in all 59 pre-natal sharks specimens examined. In one litter, sourced from a 380 cm L_T female in October (austral spring), 32 of 33 individuals (size range 69 – 75.5 cm L_T) had already developed the birth band, indicating that these pups were probably nearing birth (Figure 4.6 a). This litter also contained one 'runt' (41 cm L_T), probably already deceased upon capture, which had

one pre-birth mark just formed near the edge of the centrum. Although pre-birth marks were obvious in pre-natal and YOY samples (Figure 4.6 b), they became considerably more difficult to identify in older individuals.

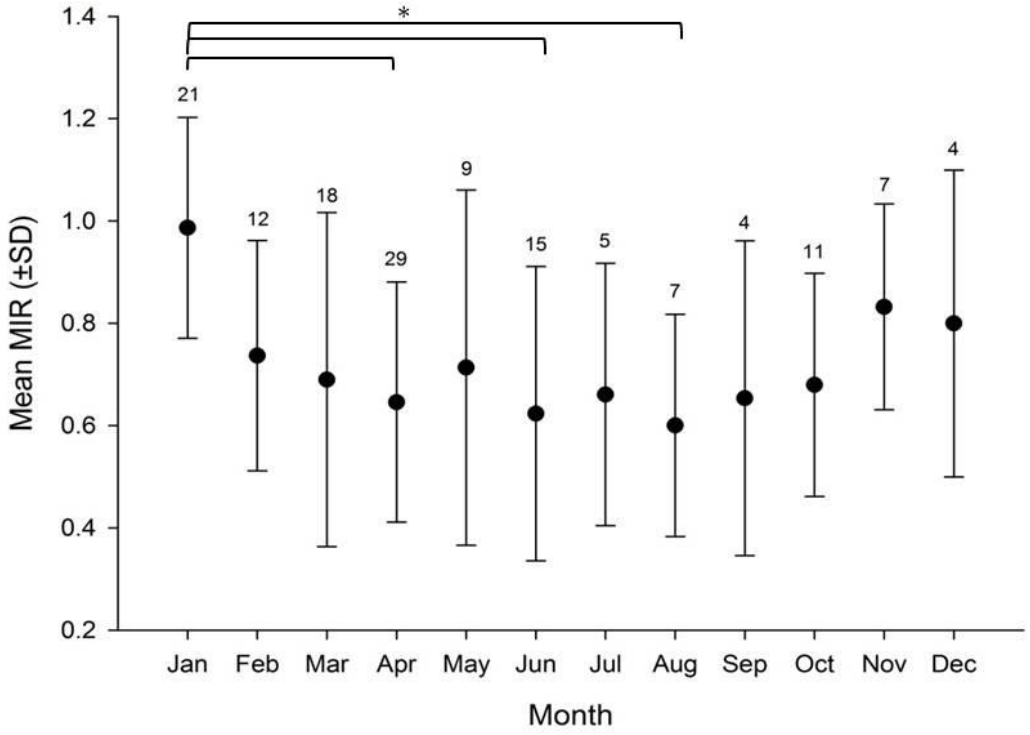

Figure 4.5: Monthly mean marginal increment ratios (MIR ± SD) and sample size per month for *G. cuvier* in east coast Australian waters. Readability scores 1–3 only, *n* = 142. Significantly different monthly means depicted by (*).

4.4.4 Vertebral features

Vertebral growth-band readability in large *G. cuvier* was difficult due to the clustering of annuli along the centrum edge. Anomalies such as split and subtle banding were also observed in a range of samples along the corpus calcareum, intermedialia, or both, and were not counted as true annuli (Goldman, 2005; Goldman et al., 2012) (Figure 4.7). Patterns of narrow and wide band pair deposition were observed in many individuals, which is characteristic of elasmobranch centrum (Cailliet et al., 1983). Consistent identification of the birth band was verified through comparison of the centrum radius of YOY and full term (> 70 cm L_T) pre-natal *G.*

cuvier. The birth band radius of post-natal samples (n = 200) ranged between 2.42 and 5.49 mm, with a mean of 3.73 mm (± 0.51 mm S.D.). The centrum radius of pre-natal *G. cuvier* (70 – 78 cm L_T; n = 57) ranged from 2.74 to 4.10 mm (mean 3.54 mm; ± 0.31 mm S.D.). Early YOY sharks (92 – 111 cm L_T ; n = 4) had centrum radius measurements ranging from 5.35 to 6.46 mm (mean 5.80 mm; ± 0.48 mm S.D.). Since the mean birth band radius for post-natal sharks fell between the mean centrum radii of pre-natal and YOY *G. cuvier*, consistent identification of the birth band was achieved (Kneebone et al., 2008). Vertebral sections that were assigned a readability score of 5 were discarded from the growth modelling (37 samples). To avoid pseudo-replication of pre-natal samples due to large litter sizes, a sub-sample of four males and four females from each of the three litters were randomly selected (n = 24) and combined with the post-natal data. Final ages were therefore determined from 178 post-natal (100 female, 67 male and 11 unsexed) and 24 pre-natal (12 female and 12 male) centra. The smallest pre-natal female and male included in the modelling analyses were 71 cm and 72 cm $L_{T,}$ respectively.

4.4.5 Age estimation and growth rates

For all counts, between-reader APE and CV were 16% and 23%, respectively. PA between the primary and secondary readers indicated that 85% of all counts differed by two or fewer bands, and 65% by one or none. The age-bias plot showed that the secondary reader assigned higher age estimates for specimens up to 12 years, and that the highest variability came from age estimates derived from older sharks (Figure 4.8).

Of the six candidate growth functions fitted, the VB3 model attracted the strongest statistical support in describing *G. cuvier* growth for all available post-natal length-at-age data sets (Table 4.1), but produced higher than expected estimates of L_0. When the models were re-run on combined pre- and post-natal data, the VB3 growth function again had the strongest statistical support for both sexes individually and combined sexes data (Table 4.1, w = 99.31 – 100) and produced somewhat more realistic estimates of L_0. The 2-parameter models, incorporating a fixed size at birth, attracted the least statistical support of the six models. Modelled pre- and post-natal male and female growth curves indicated that after the first year males grew slightly faster until around 8 – 10 year of age, at which point male growth slowed at a faster

rate than female growth slowed. Older age classes were dominated by female sharks, whose continued growth did not produce a pronounced asymptote (Figure 4.9). The oldest female was estimated to be 33 years old at 430 cm L_T, and the oldest male was 351 cm L_T and 28 years old. The combined pre- and post-natal VB3 data produced a growth curve similar to previous vertebral ageing studies of *G. cuvier* in the northwest Atlantic (Figure 4.10).

4.4.6 Length-at-maturity

There was some difficulty obtaining both the reproductive organs and vertebrae from larger *G. cuvier* when the whole animal could not be landed, or when processing was time limited on board commercial fishing vessels or at weigh stations during game fishing competitions. Of the sharks where both vertebrae and reproductive organs were collected, the largest immature female (290 cm L_T) and male (285 cm L_T) were estimated to be 13 and 9 years of age, respectively. The smallest mature female (310 cm L_T) was 12 years old. The smallest mature male was 276 cm L_T, but vertebrae were not collected from this individual so no age estimate was obtained. As the vertebral samples from sharks around the size at maturation were conspicuously lacking, A_{50} could not be quantitatively determined and was estimated for both males and females at between 10 – 13 years. L_{50} was calculated from all specimens assessed for maturity status (n = 109). For females in this population L_{50} was calculated at 326 cm L_T, and for males at 297 cm L_T.

4.4.7 Captive sharks

Growth rates of long-term captive reared *G. cuvier* were consistent across the three individuals and ranged between 20.7 – 29.7 cm.year^{-1} (Table 4.2). Based on our VB3 modelled growth curve for *G. cuvier* on the east coast of Australia, these sharks were between approximately 5 – 10 years of age at initial capture. These annual growth rates were slightly higher than the modelled growth estimates derived from vertebral age counts for wild Australian *G. cuvier* in the same age classes. The largest shark (SW1) had the slowest rate of growth for length, but the highest for mass as she approached maturity.

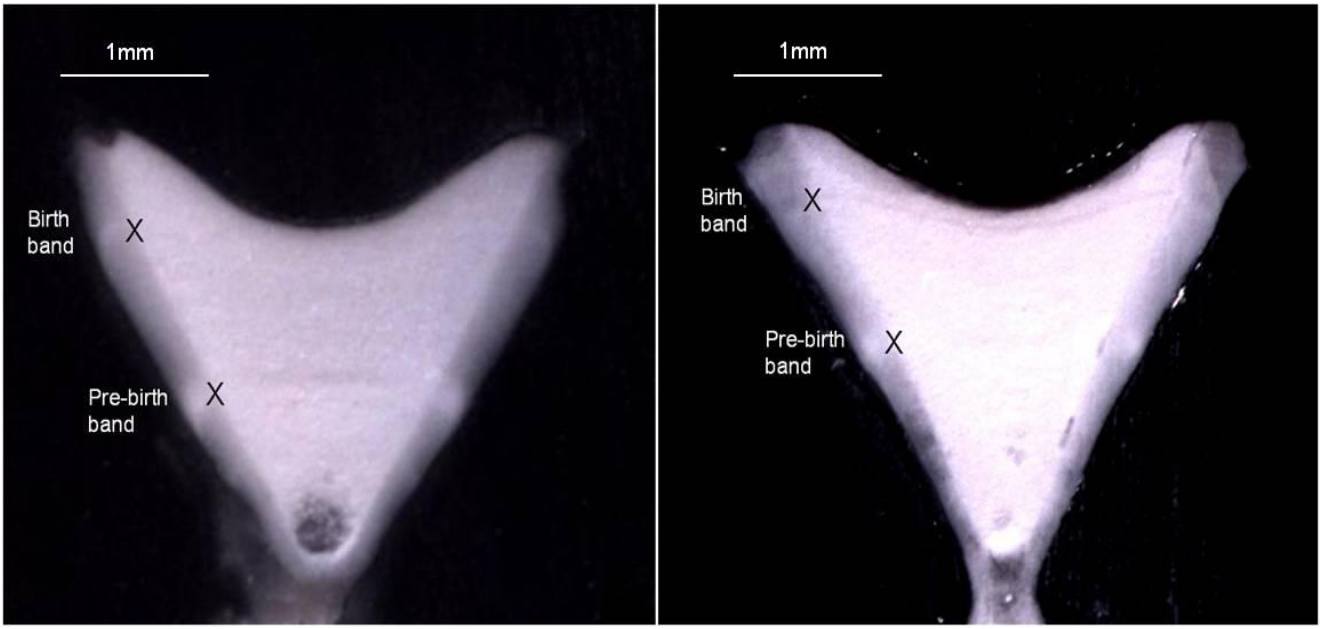

Figure 4.6: *G. cuvier* pre-birth and birth bands visible in a) pre-natal pup (female, 71cm TL), and b) young-of-the-year (female, 92 cm TL).

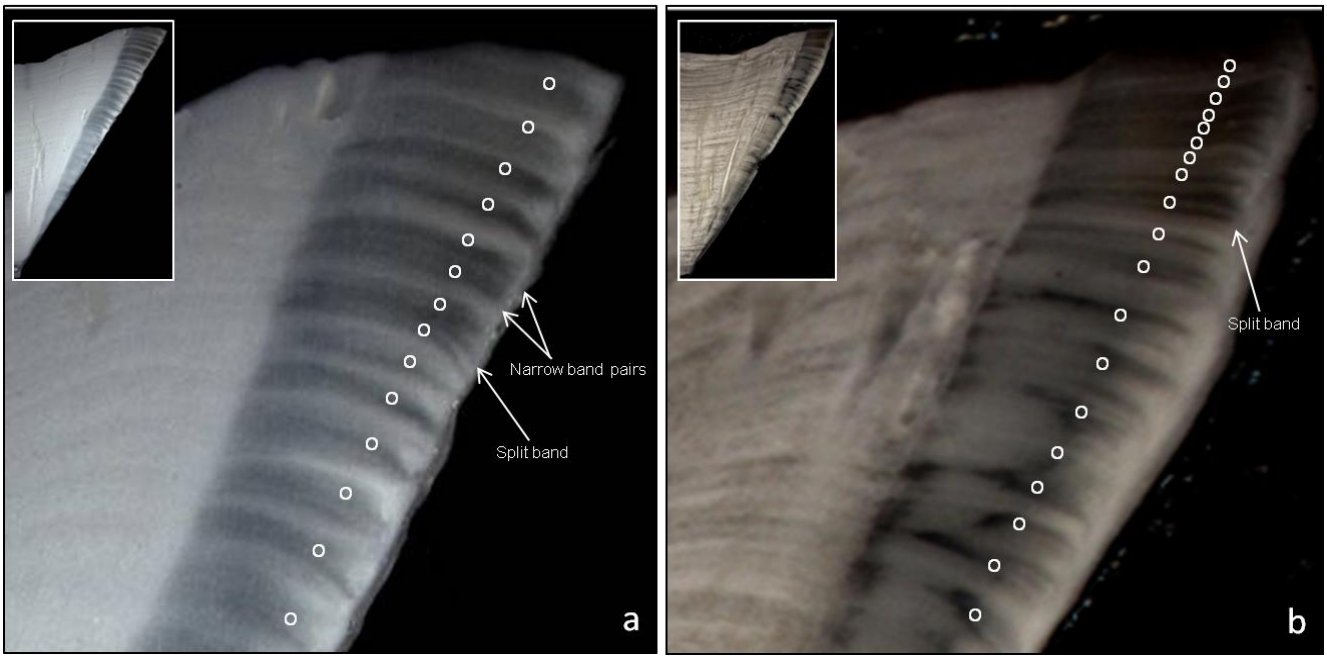

Figure 4.7: Age estimation where split or narrow band-pairs were evident on large *G. cuvier* vertebra. Images of upper corpus calcareum are from a) a 360 cm TL female; age estimated at 22 years, and b) a 345 cm TL male; age estimated at 28 years.

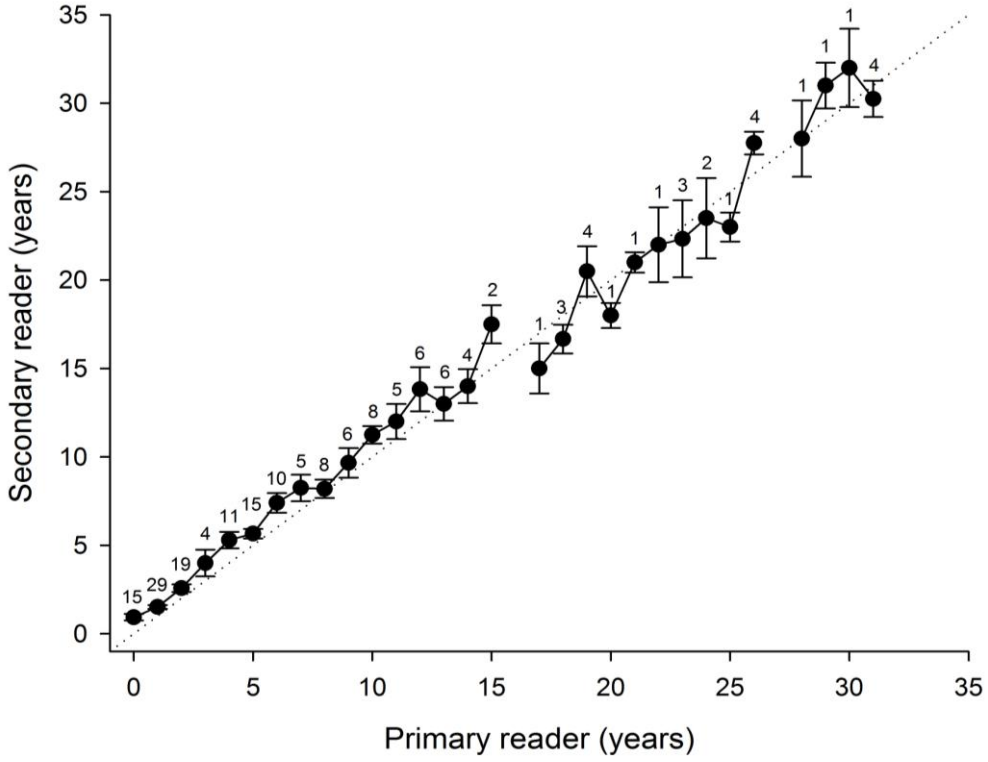

Figure 4.8: Between reader age-bias plots for *G. cuvier* vertebral age estimates. Counts are plotted relative to a line of equivalence, with error bars representing two standard errors. Numbers above data points indicate sample sizes.

Table 4.1: Growth model parameters for pre- and post-natal *G. cuvier* from the east coast of Australia. L_∞, mean age at length infinity; L_0, total length at birth; *k*, growth coefficient; AIC, Akaike's Information Criteria; Δ, Akaike score; ω, Akaike weighting; RSE, relative standard error.

	n	Model	L∞ (95% CI)	L_0 (cm) (95% CI)	*k* (95% CI)	AIC	Δ	ω	RSE
Pre- and post-natal									
Females	112	**VB3**	**418.3 (398.8 - 441.8)**	**101.5 (94.8 -108.1)**	**0.07 (0.06 - 0.08)**	**992.3**	**0.00**	**99.99**	**19.86**
	112	VB2	395.3 (379.6 - 412.4)	78	0.1 (0.09 - 0.11)	1028.4	36.04	0	23.43
	112	GOM3	394.3 (380 - 410.3)	108.2 (101.6 - 114.6)	0.12 (0.11 - 0.14)	1010.6	18.27	0.01	21.55
	112	GOM2	373.1 (359.6 - 386.9)	78	0.17 (0.16 - 0.19)	1070.0	77.66	0	28.22
	112	LOGI3	383.8 (370.6 - 397.7)	113.2 (106.5 - 119.7)	0.18 (0.16 - 0.19)	1026.6	34.30	0	23.15
	112	LOGI2	362.1 (348.2 - 375.5)	78	0.27 (0.25 - 0.29)	1102.7	110.37	0	32.66
Males	79	**VB3**	**350.5 (328.8 - 380.7)**	**101.6 (93.6 - 109.5)**	**0.12 (0.09 - 0.14)**	**714.7**	**0.00**	**99.31**	**21.62**
	79	VB2	327.3 (310.5 - 348.1)	78	0.16 (0.13 - 0.19)	739.0	24.23	0	25.35
	79	GOM3	337.1 (318.2 - 360.3)	106.7 (98.9 - 114.5)	0.17 (0.14 - 0.20)	724.7	9.98	0.68	23.02
	79	GOM2	309.1 (295.1 - 325.8)	78	0.28 (0.24 - 0.32)	759.5	44.76	0	28.87
	79	LOGI3	329.7 (312.8 - 349.9)	110.5 (102.8 - 118.5)	0.23 (0.19 - 0.27)	733.4	18.63	0.01	24.32
	79	LOGI2	296.5 (283.6 - 310.6)	78	0.43 (0.37 - 0.5)	775.0	60.23	0	31.84
Combined	202	**VB3**	**403.6 (387 - 423.9)**	**103.4 (98.2 - 108.5)**	**0.08 (0.07 - 0.09)**	**1821**	**0.00**	**100**	**21.20**
	202	VB2	376.2 (363.3 - 391)	78	0.11 (0.10 - 0.12)	1890	69.54	0	25.22
	202	GOM3	381 (367.9 - 395.2)	109.6 (104.5 - 114.6)	0.13 (0.11 - 0.14)	1852	30.93	0	22.87
	202	GOM2	353.2 (342.3 - 364.4)	78	0.19 (0.18 - 0.20)	1957	136.30	0	29.72
	202	LOGI3	370 (358.9 - 382.4)	114.3 (109.1 - 119.5)	0.18 (0.16 - 0.19)	1879	57.78	0	24.44
	202	LOGI2	339.8 (329.4 - 350.5)	78	0.29 (0.27 - 0.32)	2008	187.50	0	33.72
Post-natal only									
Females	100	**VB3**	**441.1 (417.4 - 472.9)**	**116.8 (109.6 - 123.9)**	**0.06 (0.05 - 0.07)**	**859.9**	**0.00**	**96.31**	**17.39**
	100	VB2	395.4 (379 - 414.2)	78	0.10 (0.08 - 0.11)	929.9	69.99	0	24.79
	100	GOM3	408.4 (393.3 - 427.1)	122.6 (116.2 - 129.2)	0.10 (0.09 - 0.11)	866.4	6.55	3.64	17.97
	100	GOM2	373.1 (359.1 - 387.7)	78	0.17 (0.16 - 0.19)	967.1	107.2	0	29.87
	100	LOGI3	394.1 (382 - 408.1)	127.2 (121 - 133.3)	0.14 (0.13 - 0.16)	875	15.06	0.05	18.75
	100	LOGI2	362.1 (347.7 - 376.2)	78	0.27 (0.25 - 0.3)	996.4	136.5	0	34.57
Males	67	**VB3**	**379.9 (353.4 - 420.8)**	**123.4 (115.6 - 131.2)**	**0.08 (0.06 - 0.10)**	**573.5**	**0.00**	**58.65**	**16.85**
	67	VB2	327.4 (309.6 - 349.5)	78	0.16 (0.13 - 0.2)	638.3	64.74	0	27.51
	67	GOM3	359.3 (339.9 - 385.4)	127.2 (120.2 - 134.4)	0.12 (0.10 - 0.15)	574.7	1.136	33.23	16.99
	67	GOM2	309.4 (293.9 - 326.1)	78	0.2 (0.23 - 0.33)	655.8	82.24	0	31.35
	67	LOGI3	348.7 (332.6 - 369.3)	130.4 (123.6 - 137.2)	0.17 (0.15 - 0.20)	577.5	3.953	8.13	17.35
	67	LOGI2	296.6 (282.6 - 311.7)	78	0.43 (0.37 - 0.51)	668.9	95.41	0	34.59
Combined	178	**VB3**	**433.7 (412.2 - 461.2)**	**121.5 (116.2 - 126.9)**	**0.06 (0.05 - 0.07)**	**1544**	**0.00**	**99.6**	**17.83**
	178	VB2	376.2 (386.7 - 417)	78	0.11 (0.09 - 0.12)	1690	145.2	0	26.82
	178	GOM3	400.7 (386.7 - 417)	126.6 (121.6 - 131.5)	0.10 (0.09 - 0.11)	1555	11.06	0.39	18.39
	178	GOM2	353.2 (341.9 - 364.9)	78	0.19 (0.17 - 0.2)	1749	204.2	0	31.63
	178	LOGI3	385.6 (374.3 - 398.3)	130.7 (126 - 135.5)	0.14 (0.13 - 0.15)	1570	25.24	0	19.14
	178	LOGI2	339.8 (329 - 350.9)	78	0.29 (0.27 - 0.32)	1794	249.5	0	35.90

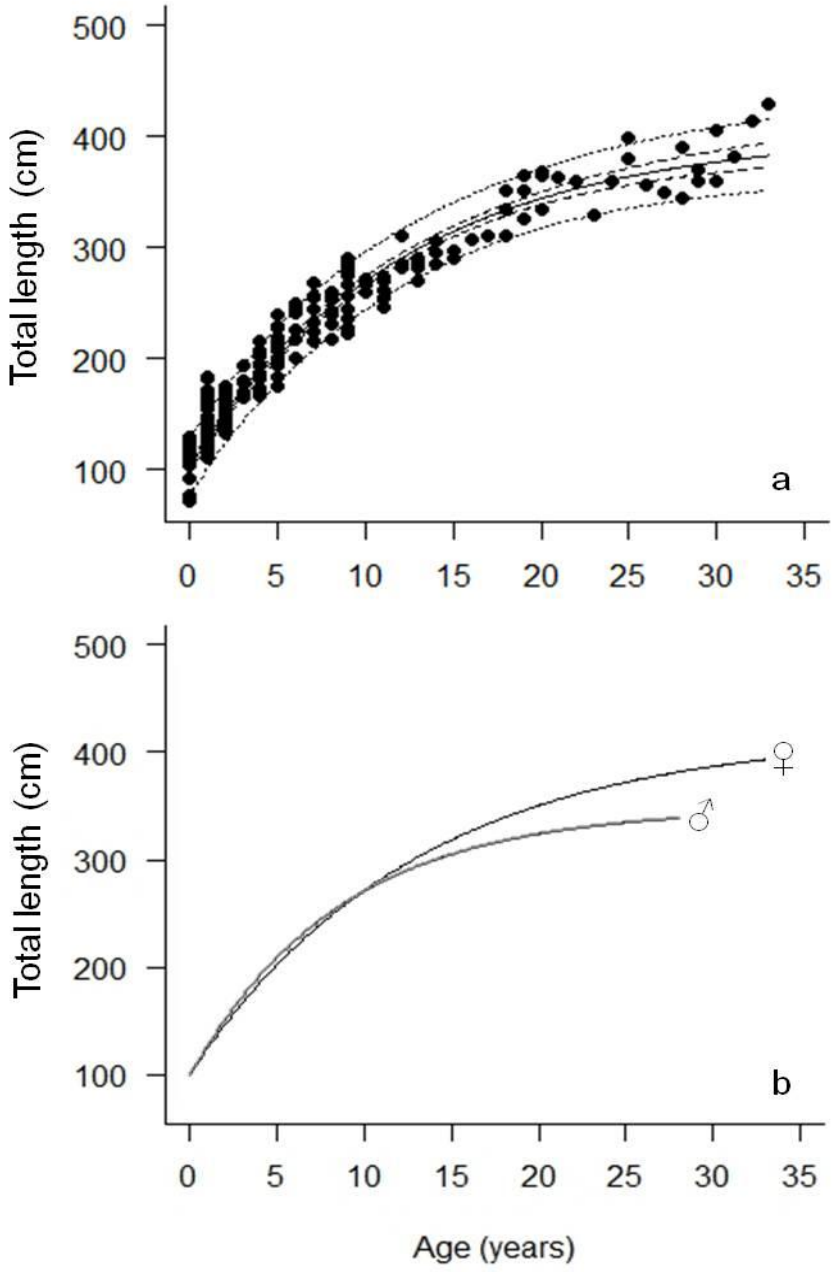

Figure 4.9: Modelled growth curves of combined sexes pre- and post-natal *G. cuvier* as determined by the 3-parameter von Bertalanffy growth function. Plots are (a) total length (cm) at age (–), with 95% confidence intervals (- - -), 95% prediction intervals (…) and raw data (●), and (b) corresponding separate female and male growth curves.

Table 4.2: Growth rate for three long-term captive *G. cuvier* held at SeaWorld (SW), Gold Coast, Australia

	Capture information				Release information					Growth rate	
#	Sex	Date	TL (cm)	Mass (kg)	Date	TL (cm)	Mass (kg)	Growth (cm)	Time (days)	cm y^{-1}	kg y^{-1}
SW1	♂	25/06/03	290	120*	24/08/04	314	240.5	24	425	20.7	103.4*
SW2	♀	16/12/03	226	62.5	12/08/04	243	102.5	17	239	26.0	61.1
SW3	♀	16/12/03	209	47.5	28/09/06	293	204.5	84	1031	29.7	55.6

*Approximate weight

Table 4.3: Regional variation of growth-model parameters for *G. cuvier*. L_∞, mean age at length infinity; *k*, growth coefficient; *n*, number of samples. Where more than one model variation was tested, results for best fit are in bold type

	De Crosta et al. (1984) Central Pacific (Hawaii)	Branstetter et al. (1987) Gulf of Mexico (USA)	Branstetter et al. (1987) NW Atlantic (USA)	Natanson et al. (1998) NW Atlantic (USA)	Wintner & Dudley (2000) SW Indian (South Africa)	Kneebone et al. (2008) NW Atlantic (USA)	Kneebone et al. (2008) NW Atlantic (USA)	Meyer et al. (2014) Central Pacific (Hawaii)	Present study SW Pacific (Australia)
Method	Vertebral ageing	Vertebral ageing	Vertebral ageing	Mark-recapture	Vertebral ageing	Vertebral ageing	Mark-recapture	Mark-recapture	Vertebral ageing
Model	VBGF	VBGF	VBGF	VBGF	**VBGF**, Gompertz	VBGF, **Gompertz**	GROTAG / Gulland & Holt	VBGF	**VBGF**, Gompertz, LGF
L_∞ (cm) TL	434*	388	440	400^	400^	425#	326#	406	403
k (year^{-1})	0.155	0.184	0.107	0.178	0.202	0.102	0.283 / 0.120	0.31	0.08
TL range (cm)	75 - 416*	91 - 355	125 - 381	99 - 338^	140 - 382^	81 - 412#	74 - 334#	96 - 384	72 - 430
n	28	25	44	42	90	238	217 / 37	37	202
Sexes	n/a	7 ♂, 10 ♀, 8 U	19 ♂, 25 ♀	17 ♂, 25 ♀	26 ♂, 64 ♀	109 ♂, 126 ♀	101 ♂, 116 ♀ / 37 U	10 ♂, 26 ♀, 1 U	79 ♂, 112 ♀, 11 U

*Converted from PCL to TL using Meyer *et al.* (2014) in Hawaii
^Converted from PCL to TL using Bass *et al.* (1975) in South Africa
#Converted from FL to TL using Kohler *et al.* (1995) in NW Atlantic

4.5 DISCUSSION

This study provides the first formal assessment of the age and growth of *G. cuvier* from the western Pacific region. Samples from the offshore gamefishing and commercial sectors provided similar numbers of male and female *G. cuvier*, while samples from shark control operations were biased toward female *G. cuvier* during this study period. Analysis of long-term QSCP catch data (1993–2014) indicates that a sex ratio bias of 1.51:1 females to males exists in this program (Holmes et al., 2012). A higher abundance of female *G. cuvier* catch was also reported in coastal waters off Western Australia, which was hypothesized to occur due to a spatial segregation of juvenile male sharks (Heithaus, 2001). Examination of large bodied *G. cuvier* specimens from offshore gamefishing operations between 2002 and 2012 in NSW revealed that significantly more male sharks were caught (1.97:1, $\chi^2 = 12.11$, $p = < 0.05$) (B. Holmes, unpubl. data), indicating that spatial segregation between immature and mature males may also be occurring on the Australian east coast.

4.5.1 Growth rates

There was some variability in model fit between the six candidate growth models applied to length-at-age data for post-natal sharks; however the inclusion of pre-natal individuals served to anchor the growth curves and provide more realistic length-at-birth (L_0) estimates. Overall, pre- and post-natal *G. cuvier* growth was statistically best described by the VB3 model. The smaller growth coefficient (k) obtained for the female and combined categories appear to be driven by the presence of five large females that were age estimated > 30 years old. This study is the first on *G. cuvier* to identify more than one individual over the age of 22, which is surprising given that *G. cuvier* are the largest of the family Carcharhinidae, and presumably amongst the longest lived (Blueweiss et al., 1978; Hoenig and Gruber, 1990). Notwithstanding, longevity estimates for *G. cuvier* reported from the northwest Atlantic range from 27 to 37 years of age (Branstetter et al., 1987; Natanson et al., 1999; Kneebone et al., 2008), indicating that a larger proportion of older sharks were sampled in this study than previously collected elsewhere, probably influencing the resultant growth coefficients for this population (for comparisons, see Table 4.3). Recent mark-recapture studies utilising the Francis maximum likelihood model (GROTAG) have

reported considerably higher growth coefficients of between 0.26 and 0.46 for *G. cuvier* from Hawaiian and NW Atlantic waters (Kneebone et al., 2008; Meyer et al., 2014), with resulting growth curves being much steeper and hence suggestive of rapid early growth and sexual maturity within the first five years. Moreover, juvenile growth rates of over 100 cm.y^{-1} for YOY were reported by Afonso et al. (2012) in Brazil and Meyer et al. (2014) in Hawaii, but these were limited to single recaptured individuals at both locations. Kneebone et al. (2008) however, using GROTAG on over 200 recaptured juvenile *G. cuvier* predominantly between 116 cm and 154 cm L_T, calculated mean growth rates of between 45.3 cm and 36.9 cm.y^{-1} for these size ranges, respectively. Previous studies comparing age-length and length-increment (tagging) data have found that growth curves are not directly comparable as VBGF parameters derived from tagging data are noticeably higher (Francis, 1988; Skomal and Natanson, 2003). Model effects such as higher L_∞ and k values derived from mark-recapture VBGF parameters may be attributed to the absence of older recaptured sharks in the sample, therefore comparison of growth rates at length may be more appropriate (Skomal and Natanson, 2003).

Captive animals are generally considered to undergo accelerated growth, with daily provisioning, regulated water condition, and energetic savings made by neither having to hunt nor avoid predators (Branstetter and McEachran, 1986). The growth rates of the Sea World sharks (between 20.7 and 29.7 cm.y^{-1}) were slightly higher than the modelled growth rate of *G. cuvier* in the same age cohorts derived from the vertebral ageing in this study (~12 – 18 cm.y^{-1}). However, the growth rates of the captive sharks were still slower than the mean annual growth rate of wild *G. cuvier* (~47.1 cm.y^{-1}) from Hawaii in similar length classes (Meyer et al., 2014). Faster linear growth in the smaller individuals (SW2 and SW3) did not correspond with a rapid increase in weight; however as SW1 approached maturity, linear growth slowed and her weight increased considerably, which appears typical for the species based on growth rates elsewhere (see Branstetter et al., 1987). While food availability has been identified as a causative factor for increased growth rates in captive *C. plumbeus* (Wass, 1971), scalloped hammerhead (*Sphyrna lewini*) (Clarke, 1971) and blacktip reef sharks (*C. melanopterus*) (Stevens, 1984a), some smaller-bodied species, such as Atlantic sharpnose sharks (*Rhizoprionodon terraenovae*) maintain growth rates that are similar to those observed in wild animals (Branstetter, 1987b). Thus, the influence of captivity on growth rates likely varies among species (Smith et al., 2004). In

addition, among wild conspecifics, significant differences in YOY growth rates from the same locality have been documented in northwest Atlantic *G. cuvier* (Natanson et al., 1999). Natanson et al. (1999) concluded that wild *G. cuvier* YOY growth rates varied considerably, and that the effect of local environmental conditions probably account for the regional differences observed for this species.

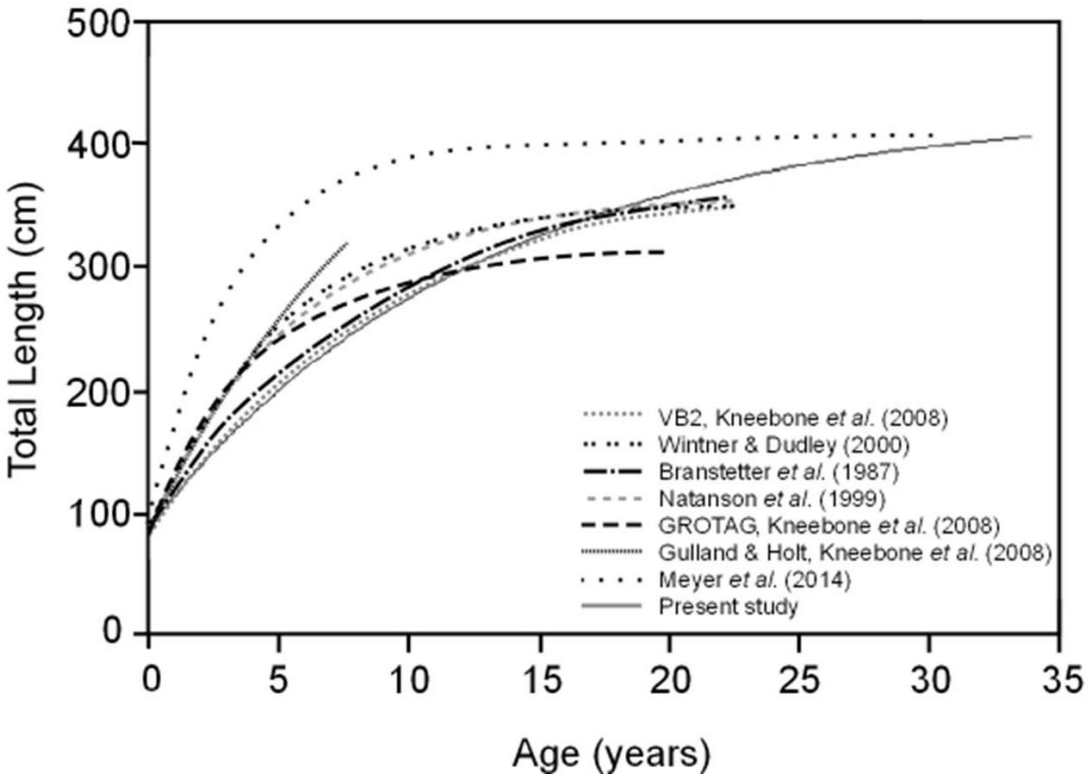

Figure 4.10: Comparison of growth curves derived from *G. cuvier* studies in different locations, using various methodologies. Growth curve for the present study is of the VB3 pre- and post-natal sexes combined.

Contrasting length-at-birth of *G. cuvier* at different locations may also influence YOY growth rates. Pup size is determined by the mother and her timing of parturition. Influences on parturition may include movement into areas of high productivity (Driggers et al., 2008), environmental stimuli, such as calcium and phosphorus uptake (Branstetter, 1987b), and temperature, with warmer waters promoting rapid pup growth that probably reduces the risk of predation (Branstetter, 1990; Norman and Stevens, 2007). Pre-mature birth or aborting of small pups can also be influenced by other external stressors, such as capture (Whitney and Crow, 2007). In the northwest Atlantic, length-at-birth has been reported to range from 45 – 50 cm L_T (Bigelow and Schroeder, 1948) to around 70 cm L_T (Clarke and von Schmidt, 1965; Branstetter et al., 1987). In the Caribbean, length-at-birth was established at 60 – 70 cm L_T (Rivera-López, 1970), while in Africa, estimated birth size was 70 cm L_T for *G. cuvier* off Madagascar (Fourmanior, 1961), and 85 cm L_T in South Africa (Wintner and Dudley, 2000). More recently, Whitney and Crow (2007) found that *G. cuvier* pups in Hawaii were born at 76 – 89 cm L_T. In Australia, *G. cuvier* length-at-birth has been identified as between 80 – 90 cm L_T (Simpfendorfer, 1992). These observed regional differences in birth size likely influence the respective YOY growth rates for that region, with smaller pups probably undergoing more rapid growth, particularly in tropical waters. Collectively, identification of whether inter-oceanic differences in growth rate are real, a consequence of sample collection methodology, or an artefact of statistical modelling, remains difficult to ascertain in elasmobranch age and growth studies.

4.5.2 Length-at-maturity

The majority of previous *G. cuvier* studies based length-at-maturity estimates on the smallest recorded mature individual. In a Florida study, Clark and von Schmidt (1965) reported that the smallest mature female was 297 cm L_T, but also found a larger 332 cm L_T female to be immature. Branstetter et al. (1987) found the smallest mature females were 325 cm L_T (8.8 years) and 318 cm L_T (9 years), and the smallest mature males were 310 cm L_T (8 years) and 312 cm L_T (10.1 years), in the Gulf of Mexico and the NW Atlantic, respectively. In Africa, Wintner and Dudley (2000) reported the L_{50} and A_{50} for females at 349 cm L_T and 11 years of age, and 320 cm L_T and 8 years for males, respectively. Of the two mature females observed in their study, the youngest mature female (8 years; 380 cm L_T) was actually larger in size than the older female (13 years; 372 cm L_T). In the current study, L_{50} for females (326

cm L_T) and males (297 cm L_T) was smaller than that reported in South Africa, although age-at-maturity was slightly higher being estimated between 10 – 13 years for both sexes.

4.5.3 Pre-birth banding

Pre-birth marks have been shown to occur in the centra of several placental shark species, with mark formation taking place when observed embryo lengths are consistent with placenta formation and attachment (sandbar shark (*Carcharhinus plumbeus*), Casey et al., 1985; blacktip shark (*C. limbatus*) and spinner shark (*C. brevipinna*), Branstetter, 1987a; bull shark (*C. leucas*), Branstetter and Stiles, 1987), or when increases in calcium and phosphorous levels were observed, also around the time of placentation (*C. amblyrhynchos*, Radtke and Cailliet, 1984). However, pre-birth marking in aplacental species such as *G. cuvier* has been less thoroughly described and is more difficult to define. Pre-birth marks in the vertebrae of two other aplacental species, the shortfin mako (*Isurus oxyrinchus*), and the grey nurse shark (*Carcharias taurus*), were surmised to be caused by embryonic changes in nutrition associated with the switch from feeding on nutritive eggs (oophagy) to consuming the large quantities of yolk reserves in the neonate stomach (Branstetter and Musick, 1994; Ribot-Carballal et al., 2005). Information concerning the embryonic processes of *G. cuvier* is somewhat limited (Schwartz, 1994), with only one previous study documenting the presence of branchial filaments on the gills and spiracles in early embryo *G. cuvier*, presumably functioning as an absorption point for the nutritive liquid in the shell membrane sac (Sarangdhar, 1943). In the later stages these filaments disappear and nutrition then appears to be supplied by a large external yolk sac, which, through the hepatic portal duct, is also connected to an internal yolk-sac that supplies nutrients to the pup in the few days post-partum (Sarangdhar, 1943). These embryonic changes constituting a shift in nutrition may therefore cause pre-birth centrum marks in *G. cuvier*. Although previous vertebral ageing studies on *G. cuvier* have not identified pre-birth marks, these studies had few or no pre-natal or neonatal individuals (Branstetter et al. (1987), $n = 2$; Wintner and Dudley (2000), $n = 0$; Kneebone et al. (2008), $n = 8$). Notwithstanding, all 59 pre-natal vertebrae examined in this study displayed at least one obvious embryonic mark in the centrum, with some near-full term pups also displaying an additional band near the edge of the centrum, which is consistent with the location of the birth band. Assuming a 15 – 16

month gestation period (Whitney and Crow, 2007) with parturition in the austral summer (December – February; Simpfendorfer, 1992a), it may be that the first pre-birth marks observed in these litters are indeed winter annuli, formed around June when pups are approximately 35 – 40 cm L_T. This is consistent with the observation of a winter annulus near the edge of the centrum in the smallest examined embryo (41 cm L_T). The formation of winter annuli in *G. cuvier* was first described by Branstetter et al. (1987), with the first winter annulus post-partum representing approximately 6 months of growth. Pre-birth marks became difficult to identify in the vertebrae of *G. cuvier* beyond YOY, probably due to the progressive calcification of the vertebral column that occurs through thickening of the mineralized cartilage of the intermedialia (Clement, 1992). Changes in calcification may also be linked to ontogenetic stages of progressively more mineralised tissue (Dean and Summers, 2006), which occurs post-partum.

4.5.4 Age estimation

The identification of narrow and split banding patterns, particularly in older *G. cuvier*, increased the difficulty associated with determining true annuli in this species. Although split banding has been described as 'background noise' (Goldman, 2005), and that periodic annuli deposition should have some kind of 'consistency' (Goldman et al., 2012), it is possible that the ageing protocols used in both this and previous vertebral ageing studies have resulted in some age underestimation for *G. cuvier*. Casey et al. (1985) acknowledged potential underestimation of *C. plumbeus* ages by not counting the narrow rings near the outer margin of the vertebrae as annuli, because they did not fit the 'criteria' for an annual mark as validated by the younger size classes. Casey and Natanson (1992) then revised the earlier estimates using mark-recapture data, finding that vertebral counts using conservative protocols grossly underestimated the longevity estimates for the species. Branstetter et al. (1987) and Kneebone et al. (2008) both acknowledged difficulties in counting annuli along the periphery of centra in large *G. cuvier*, but neither provided images of vertebrae that highlighted this outer edge region to allow the reader to evaluate the methodology used. Despite vertebral ageing being the most widespread method to assess shark age and growth (Cailliet, 1990), recent studies employing bomb radiocarbon analyses have found that the age of large individuals may be underestimated, predominantly due to band deposition slowing or ceasing in large, older sharks. Francis et al. (2007)

reported that the age of porbeagle sharks (*Lamna nasus*) may have been underestimated by as much as 50%. More recently, Natanson and Skomal (2015) reported that white shark (*Carcharodon carcharias*) band-pairs appeared narrow, grouping together to form the broader band pairs observed on the lower portions of the centra of larger specimens. This observation is akin to the presence of both narrow band-pairs and split banding we observed in the *G. cuvier* vertebrae, which did not fit the criteria of an annual growth band-pair in this study, and were not counted as such. While not described in the text, evidence of split banding in *G. cuvier* vertebrae was also shown in Figure 1 of Kneebone et al. (2008), who also assigned these as a single band-pair representing one year of growth. The close association of the *G. cuvier* and reference radiocarbon chronologies in the northwest Atlantic study suggested that major under ageing (> 3 – 6 years of absolute age) was unlikely, at least up to the age of 20. While this gives us some confidence in our age assignment in smaller specimens, our estimates based on band-pair counts of 18 large sharks aged > 20 years in this study may still be underestimated as validation has not been achieved over the species entire size range (Natanson et al., 2014; Hamady et al., 2014). Notwithstanding, the current study provides a reasonable estimate of maximum age (33) through vertebral band-pair counts, fitting with the proposed longevity estimates of between 27 – 37 years of age reported elsewhere (Branstetter et al., 1987; Natanson et al., 1999; Kneebone et al., 2008).

Another explanation for split banding may be that differences in cartilage mineralisation occur during different growth phases (Cailliet et al., 1983). Jones and Geen (1977) suggest that patterns of mineralisation may be strongly influenced by seasonal environmental changes therefore affecting growth rates. The cells of vertebral cartilage undergo a progressive change in shape from the flattened and fusiform cells deepest in the structure, to the ovoid cells just being incorporated into the mineralising front. This change in shape may depend on the time and site of inclusion, and can be explained by the effect of local tissue pressure at the time of the cells' growth and incorporation (Clement, 1992). We might consider that the variation in mineralisation patterns, and the incorporation of these cells during growth, may contribute to observed split banding patterns in *G. cuvier* vertebrae. However, to date, little is known about the interaction between the different forms of calcification in the vertebral cartilage of sharks, nor how these processes vary with age, species, or feeding behaviour (Dean and Summers, 2006). These findings reinforce the

importance of age validation in elasmobranch studies, particularly when population assessments and management regimes are often based on life-history information (Harry et al., 2013).

4.5.5 Validation

Validation of absolute age in elasmobranch fishes is particularly difficult; therefore most studies attempting validation do so by focusing on validating the temporal periodicity in growth increment formation (Cailliet and Goldman, 2004). Fish can be marked externally, or injected with chemicals so as to leave a permanent mark on the calcified structures used for ageing. However these approaches are not well suited to long-lived species since recapture rates of old fish tend to be low (Campana, 2001), and failure of chemical marking in the vertebrae of large sharks with little or no somatic growth may occur (Harry et al., 2013). Moreover, the extent of movements by highly mobile shark species in some regions limits the chances of re-encountering the same individuals at a later date. For example, off the east coast of Australia *G. cuvier* have been demonstrated to move distances of up to 2000 km across the southwest Pacific in just over one month (Holmes et al., 2014). Additionally, the NSW Game Fishing Tagging Program has tagged 1083 *G. cuvier* off the Australian coast since 1973, with only 26 recaptures up to 2014 (~2.4% recapture rate; NSW DPI, unpubl. data). In lieu of accurate recapture data or chemically marked individuals, MIR analysis of annulus periodicity has been used as a way to verify annulus formation in *G. cuvier* ageing studies, with mixed success. Branstetter et al. (1987) demonstrated that one growth band, consisting of one calcified opaque zone and one less calcified translucent zone, formed annually in *G. cuvier* from the northwest Atlantic and Gulf of Mexico. However, Wintner and Dudley (2000) found no clear trend in the MIR analysis conducted on *G. cuvier* in South Africa, but suggest that the larger MIR range observed in spring may represent transition from one growth ring to the next, indicating annual growth band deposition. The MIR analysis undertaken in the current study showed that annuli were farthest from the centrum edge in the austral summer (January), and closest during the austral winter (June – August). The MIR trends indicate that *G. cuvier* off the east coast of Australia also form one growth band each year, most likely in late spring/summer. This is consistent with the austral summer pupping season in this region (Simpfendorfer, 1992a). Other validation techniques to verify and/or validate annual band deposition

in *G. cuvier* have also been used. In Hawaii, DeCrosta et al. (1984) assumed annual periodicity based on the close agreement of growth curves derived from vertebral counts and length frequencies. Wintner and Dudley (2000) also chemically marked and recaptured three *G. cuvier* in South Africa, finding annual growth band deposition in young age classes (< 5 years). More recently, the bomb radiocarbon analyses undertaken on *G. cuvier* in the northwest Atlantic (Kneebone et al., 2008) validated annual band deposition in individuals up to age 20. Based on these collective findings and the results of the MIR analysis of the current study, we assume that the number of vertebral growth bands is representative of year classes for *G. cuvier* on the east coast of Australia.

Individual variation in growth is typical for *G. cuvier* across their geographic range (Meyer et al., 2014; Natanson et al., 1999), which partly explains the differences in the observed growth curves from different populations. These regional variations in life history traits highlight the need to obtain local life history information in order to determine fecundity, growth rate, mortality and subsequent susceptibility to fishing pressure before appropriate management regimes may be implemented. The southwest Pacific population of *G. cuvier* sampled in the present study exhibited a slower rate of growth and slightly higher age at sexual maturity than reported elsewhere, indicating that recovery from depleted stocks may take longer in this region. This may explain why recent catch rate trends of *G. cuvier* in southeastern Australia have shown significant declines (Park, 2009; Reid et al., 2011; Holmes et al., 2012), when other regions are reporting increasing abundances (Dudley and Simpfendorfer, 2006). We must also consider that sample size, protocol methodology, verification and validation can also have considerable influence on regionally-specific growth model results (Cailliet and Goldman, 2004; Goldman, 2005). Justification of ageing methodology will also be aided by a greater understanding of the mineralisation processes associated with vertebral band deposition, which are integral in understanding the effect that anomalies such as split-banding have on vertebral age determination processes. For future studies, we encourage ongoing efforts to gain regionally specific growth estimates and promote greater transparency regarding the difficulties associated with vertebral ageing studies in elasmobranchs, particularly for larger species.

4.6 ACKNOWLEDGEMENTS

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Chapter 5: Reproductive strategies of the tiger shark (*Galeocerdo cuvier*) in the western Pacific Ocean

5.1 ABSTRACT

Understanding the reproductive strategies of commercially- and recreationally-exploited elasmobranchs is fundamental in implementing appropriate fisheries management regimes. The tiger shark (*Galeocerdo cuvier*) is the only carcharhinid with an aplacental viviparous reproductive mode. We present the first analysis of the reproductive biology of western Pacific tiger sharks from specimens obtained from the Queensland Shark Control Program (QSCP) between 2008 and 2011, complemented by additional samples from New South Wales (NSW) game fishing tournaments between 2010 and 2013. Reproductive seasonality and cycle were estimated through historical QSCP data from 1993 – 2014. Pups (n = 112) from four pregnant sharks were used to assess the possibility of multiple paternity. Male clasper length and female oviducal gland width provided the best measures to determine maturation in this species. Length at 50% maturity (L_{50}) was 297 cm TL for males and 325 cm TL for females. Litters sizes (n = 83) ranged from 5 to 92 pups (26 ± 14, mean and SD), and birth is in the austral summer after a gestation period of around 15 – 16 months. Female sharks that were pregnant, or had well-developed oocytes, or had small oocytes were found throughout the year, consistent with a triennial breeding cycle. There was no evidence of multiple paternity, which may have implications for the genetic diversity of this population.

5.2 INTRODUCTION

The tiger shark (*Galeocerdo cuvier*) (Péron and Lesueur 1822) is the largest species in the family Carcharhinidae, with a circumglobal distribution in both tropical and warm temperate neritic and pelagic waters. Off the Australian east coast, *G. cuvier* maintain variable home ranges, with movements extending across the broader Indo-West Pacific into both tropical and seasonally warm temperate waters (Holmes et al., 2014). Throughout the region *G. cuvier* is targeted primarily by recreational shark game fishers and by shark control programs, and is also taken by commercial fishing operations (Pepperell, 1992; Holmes et al., 2012). Illegal foreign fishing vessels, particularly in the Coral Sea, also target large tiger sharks for their high value fins (Marshall, 2011). To date, the management arrangements for the species in Australian waters were developed using a pre-cautionary approach given the paucity

of information regarding its biology and general life history characteristics in the region. In order for quantitative stock assessments to be conducted to refine management actions, reproductive parameters such as sex ratio at birth, number of offspring, age or size-at-maturity, reproductive seasonality and cycle, and gestation period are all specific parameters required for fishery assessment models (Walker, 2005).

Tiger sharks are the only carcharhinid with an aplacental viviparous (ovoviviparous) reproductive strategy (Whitney and Crow, 2007). While reproductive data on this species from Australian waters remain scant, selected aspects of tiger shark reproductive biology have been studied elsewhere. Size-at-maturity estimates for males from southern Africa, the northwest Atlantic, and from around Hawaii mature at 290 – 310 cm TL (Fourmanior, 1961; Clarke and von Schmidt, 1965; Branstetter et al., 1987; Whitney and Crow, 2007). Female sharks appear to mature at similar (287 – 310 cm TL, (Clarke and von Schmidt, 1965; Branstetter et al., 1987; Simpfendorfer, 1992a)) or slightly larger sizes (330 – 345 cm TL, (Fourmanior, 1961; Wintner and Dudley, 2000; Whitney and Crow, 2007)), although there is a questionable early report of maturity at 210 cm TL from Brazil (Alves, 1977). Mean litter sizes of 21 – 50 embryos have been reported (Bigelow and Schroeder, 1948; Fourmanior, 1961; Rivera-López, 1970; Bass et al., 1975; Aitken, 2003; Whitney and Crow, 2007), with the relationship between embryo number and maternal length found to be positively correlated in one study (Simpfendorfer, 1992a), but not in others (Aitken 2003; Whitney and Crow, 2007).

Determination of the gestation period has been hampered by an inability to obtain relevant data for large numbers of pregnant sharks. Early studies suggested a gestation period of slightly over 12 months duration, but were limited to records from four to 16 litters (Springer, 1938, 1940; Clarke and von Schmidt, 1965; Rivera-López, 1970). Whitney and Crow (2007) estimated gestation to last 15 – 16 months in Hawaiian tiger sharks based on analysis of 23 litters, and found both early- and late-term embryos within the same calendar month suggestive of a gestation period of well over a year. North Atlantic tiger sharks were surmised, however, to probably have a gestation period of 12 months (Castro, 2009). This was based on the observation of tiger sharks carrying both unfertilised eggs and near-term young in May (boreal spring), indicating that females are possibly reproductively synchronous in this region. Castro (2009) concluded that differences in reproductive strategies may exist

between Atlantic and Pacific *G. cuvier* populations. The timing of parturition varies and is often estimated, based on observations of females carrying near-term embryos. Pupping reportedly occurs in the spring and early summer. In Brazil, late-term embryos have been found from May to August (Alves, 1977), while in North Carolina, Schwartz (1989) reported the pupping season to occur from July – September. In Hawaii, Whitney and Crow (2007) state that pups are born between September – October. In the southern hemisphere, Simpfendorfer (1992) reported summer (December – February) parturition in northeastern Australia.

Contrasting size-at-birth estimates for tiger sharks at different localities also has the potential to influence accurate determination of pupping season. In the northwest Atlantic, size-at-birth has been reported to range from 45 – 50 cm TL (Bigelow and Schroeder, 1948) to around 70 cm TL (Clarke and von Schmidt, 1965; Branstetter et al., 1987). In the Caribbean, Rivera-Lopez (1970) established a size-at-birth of 60 – 70 cm TL, while in Africa, Fourmanoir (1961) estimated birth size at around 70 cm TL for tiger sharks off Madagascar, and Wintner and Dudley (2000) reported 85 cm TL in South Africa. Whitney and Crow (2007) found that tiger shark pups in Hawaii are born at 76 – 89 cm TL. In Australia, tiger shark size-at-birth has been reported as 80 – 90 cm TL (Simpfendorfer, 1992a). This variation in birth size may be related to possible regional sub-populations, variable gestation length, seasonality of reproductive events, or biases due to sample acquisition.

The reproductive cycle of the tiger shark remains one of the least understood aspects of its reproductive biology. Until recently, most studies proposed a biennial reproductive cycle (Rivera-López, 1970; Alves, 1977; Branstetter et al., 1987), and that mating appeared to occur before full-term females had pupped (Branstetter et al., 1987). In the first study to examine a large number of mature females, Whitney and Crow (2007) inferred a triennial breeding cycle supported by the observation that the proportion of captured sharks that were pregnant was lower than would be expected for a biennial reproductive cycle. In order to fully understand the complete reproductive strategy of *G. cuvier*, a greater understanding of the function of sperm storage in the oviducal gland is also required. Sperm storage in the oviducal glands of tiger sharks was first reported by Prasad (1945), and later refined by Pratt (1993), who suggested that the long-term storage interval identified is likely to be at least the gestation period. In addition, repeat fresh inseminations are probably required for highly migratory, semi-solitary species like the tiger shark, in order to increase the

chance of fertilization in the absence of male contact (Pratt, 1993). To date, there is still no information available as to whether sperm from different males can be stored to facilitate genetic diversity among litters in this species.

Multiple paternity has been studied in a range of elasmobranchs (see Byrne and Avise, 2012 for review), with three species of carcharhinids assessed to date (*C. altimus* and *C. galapagensis*, Daly-Engel et al., 2006; and *C. plumbeus*, Daly-Engel et al., 2007; Portnoy et al., 2007). Multiple paternity was found in single litters of *C. altimus* and *C. plumbeus*, but not in the single *C. galapagensis* litter, potentially escaping detection due to the small sample size (Daly-Engel et al., 2006). Such studies on polyandry and multiple paternity enables patterns of reproductive behaviour to be inferred in the absence of direct behavioural observation (Fitzpatrick et al., 2012a), which is particularly important in the study of wide-ranging highly mobile species like the tiger shark.

The current study involves an analysis of the reproductive biology of *G. cuvier*, including a genetic examination of possible multiple paternity. Historical information from the Queensland Shark Control Program (QSCP) is also used in an evaluation of the reproductive cycle and gestation period for the species in the western Pacific Ocean.

5.3 Materials and Methods

5.3.1 Sample collection

Tiger shark reproductive samples, including pups from pregnant sharks, were collected from shark caught in the QSCP between 2008 and 2011, and from sharks caught by NSW recreational game fishers between 2010 and 2013 (Figure 5.1). The QSCP uses nets and/or drumlines positioned adjacent to popular bathing locations at 10 areas (85 beaches) along the Queensland east coast. QSCP specimens for biological analyses were provided either whole, or reproductive organs were removed from the carcass and stored separately. All samples were stored frozen at -20°C prior to transport. Fishing contractors record information relating to gear type, species caught, total length (±1 cm), sex, number of pups, stomach contents, and mortality state. Historical data from 1993 – 2014 was used to calculate the reproductive seasonality and length of gestation for pregnant sharks by calculating mean monthly embryo length (cm) and comparing with the TL of free-swimming neonates on a

monthly basis. The female reproductive cycle was assessed by calculating the percentage of mature females pregnant by month, based on the length at which 50% of the females are mature (L_{50}) (Mollet et al., 2000). The L_{50} was determined for each sex using 50 cm TL size classes, with reproductive state calculated from the maximum oocyte diameter (MOD), ovary and oviducal gland mass of females; and from clasper length and calcification state for males (Conrath and Musick, 2002; Walker, 2005; Whitney and Crow, 2007). A least-squares non-linear regression (PASW Statistics V.18) using the logistic function

$$P(l) = 1 \cdot \left(1 - e^{-\ln(19)\left(\frac{l-L_{50}}{L_{95}-L_{50}}\right)}\right)^{-1}$$

(Walker, 2005)

enabled calculation of parameter estimates. $P(l)$ is the proportion of mature animals at TL l, and the lengths at which 50% and 95% of the population is mature are represented by L_{50} and L_{95}, respectively (Gutteridge et al., 2013).

5.3.2 Processing of biological tissue

For most sharks, capture date and location, TL (±1 cm) and sex were recorded. Total length was determined by allowing the caudal fin to take a natural position. For whole sharks obtained from the QSCP, fork length (FL), pre-caudal length (PCL) (±1 cm) and body mass (M) (±500 g) was also recorded. For sharks captured by NSW game fishers, TL was provided for all samples, while FL and M were only available for some specimens. Where FL or M were not recorded, proxy values were calculated using length-length and length-mass conversions for this population (Holmes et al., In press). A chi-square goodness-of-fit test was conducted to determine whether there was a sex-bias within this population (PASW Statistics V.18). A Shapiro-Wilk test for normality was conducted to determine whether the size-frequency distribution of either sex was skewed.

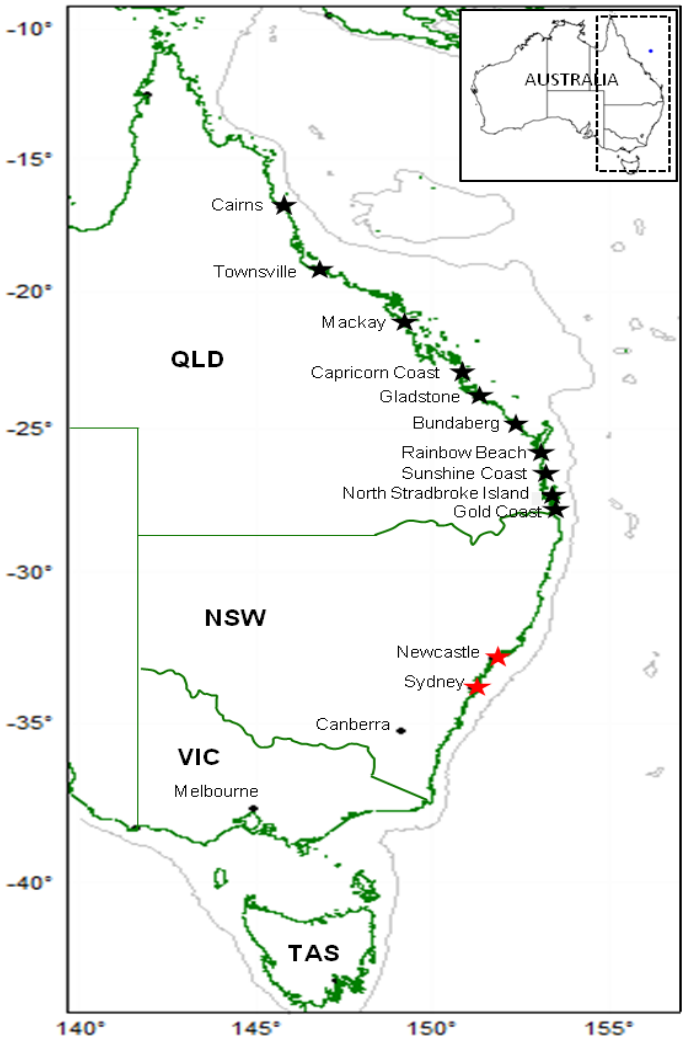

Figure 5.1: Map of study area on the east coast of Australia. Black stars indicate QLD QSCP locations where *G. cuvier* was sampled. Red stars indicate where samples were obtained from gamefishing competitions in NSW.

Maturity state was determined from measurement of clasper length and calcification state for males. Inner and outer clasper lengths were measured from the tip of the clasper to the anterior margin of the cloaca or pelvic fin fold, respectively (Whitney and Crow, 2007). Clasper length (cm) was plotted against TL (cm) to determine size at maturity. For female tiger sharks, ovary mass (g), oviducal gland width (mm), maximum oocyte diameter (MOD) (mm), litter size and number of oocytes were potted against TL (cm) to determine the onset of maturation and reproductive cycle. Litter characteristics such as number of pups, sex ratio, and pup TL, FL, PCL (± 1 mm) and M (± 0.5 g) were recorded from four pregnant sharks.

Lengths were measured with sharks in a natural position, measuring from the tip of the snout to the tail on the underside of each specimen. Each shark was weighed whole. Pup internal yolk sacs were weighed (g) and plotted against pup size for three of the litters to investigate variation in yolk sac mass among and between litters.

5.3.3 Multiple paternity

Genotypes were obtained from the fin clips of 112 embryos from four litters (63 female, 49 male) to test for multiple paternity among pups using nine microsatellite loci developed for tiger sharks (see Bernard et al., 2014). The maternal genotype was not available for one litter. Litter sizes ranged from 16 to 36. Tissue was stored in 95% ethanol until laboratory processing. DNA extraction was performed using a phenol/chloroform extraction (Chomczynski and Sacchi, 1987), with loci optimised into polymerase chain reaction (PCR) multiplexes using M13 fluoro-tagged primer sequences described in (Williams et al., 2014). Multiplex 1 consisted of loci tgr_1157, tgr_212, tgr_47, tgr_233, tgr_348; and, multiplex 2 consisted of tgr_1033, tgr_1185, tgr_891 and tgr_943. The samples were amplified using a 14 µl PCR mixture containing 10 ng of genomic DNA, 8 µl of master mix (1x Kapa Buffer A, 1.5% DMSO, 0.18 mM dNTP, 0.25 M Betaine, 0.8 units/reaction Taq), and 4 µl of primer mix (3µl forward, 30 µl reverse, 30 µl M13-fluoro, 87 µl H_2O) . Loci were amplified in 2 multiplexes using the following protocols: Multiplex 1; 94°C for 2 min, followed by 12 cycles of 94^{o}C for 15 s, 56°C for 30 s and 72°C for 45 s, with the annealing temperature reduced by 0.5^{o}C each cycle (touchdown cycle). The reaction was then exposed to 23 cycles of 94°C for 15 s, 50°C for 30 s and 72°C for 45 s. Multiplex 2; 94°C for 2 min, followed by 10 cycles of 94°C for 15 s, 60°C for 30 s and 72^{o}C for 45 s, reduced by 0.5^{o}C each cycle. The reaction was then exposed to 23 cycles of 94^{o}C for 15 s, 55^{o}C for 30 s and 72^{o}C for 45 s. The reactions for both multiplex 1 and 2 completed at 72°C for 7 min before being held at 4^{o}C until required for further analysis. Amplicons were diluted 60-fold and then gel separated by capillary electrophoresis (Applied Biosystems 3130xl) following the manufacturer's recommendation. Alleles were sized against an internal size standard (GeneScan-500 LIZ) before being scored using GeneMapper version 5.

To confirm that the microsatellite loci were suitable for multiple paternity testing, we genotyped 34 adults randomly sampled along the east coast of Australia. We estimated the number of alleles, unbiased expected heterozygosity, and the probability

of identity of siblings (PIDsib) using GenAlEx 6.5 (Peakall and Smouse, 2005; Peakall and Smouse, 2012). Genotypes were checked for null alleles and scoring errors using Micro-Checker 2.2.3 (Van Oosterhout et al., 2004). We tested for Hardy Weinberg equilibrium (HWE) in the adult east coast population using the Markov chain method in GENEPOP 4.1.3 (Raymond and Rousset, 1995), with 100,000 dememorisation steps, 100 batches and 10,000 subsequent iterations. We also tested for linkage disequilibria among loci using an exact test based on a Markov chain method as implemented in GENEPOP, in both cases using sequential Bonferroni to correct for multiple tests ($p < 0.05$) (Rice, 1989).

To determine our power to detect multiple paternity we performed simulations using PrDM 1 (Neff and Pitcher, 2002). This software calculates the probability of detecting multiple mating given: 1) allele frequencies in the adult population; 2) differing litter sizes; and 3) differing multiple paternity rates. We simulated three multiple paternity scenarios: 1) two fathers equal paternity (50% each); 2) two fathers moderate skew (66%, 33%); and 3) two fathers high skew (92.5%, 7.5%). The 'high skew' scenario represents approximately one pup with a different father in a litter of 15. Simulations were performed for the litter size range of our study, using allele frequencies estimated from the Australian east coast population (34 adults) and assuming maternity was unknown.

Paternity of litters was determined using two methods; manual allele counting (see also Avise et al., 2002; Chapman et al., 2004; Hernandez et al., 2014), and a full pedigree likelihood method, executed in Colony 2.0.5.5 (Wang, 2004; Jones and Wang, 2010). Manual allele counting was undertaken by subtracting the maternal alleles and identifying the number of unique paternal alleles at each locus. The total number of alleles per locus for each litter was also quantified. The presence of more than two paternal alleles across at least two loci was considered evidence for multiple paternity (Avise et al., 2002; Chapman et al., 2004; Lage et al., 2008). Colony 2.0.5.5 infers sibships and parentage based on multilocus genotypes by assigning offspring to full or half-sib families. Pedigrees for each cluster are constructed, and then pedigrees likelihoods are compared to define sibling groups. Maternal genotype was included where known (assigned with high confidence, 0.999), and a low uniform error rate was applied (0.0001).

5.4 RESULTS

5.4.1 Length-frequency and size-at-maturity

Length-frequency information for 5886 tiger sharks (3547 females, 2339 males) was obtained from QSCP adult and pup data for 1993 – 2014, which included those specimens used for the biological component of this study, and specimens from recreational game fishing operations in NSW (Figure 5.2). The sex ratio of all sharks was significantly biased towards females with a 1.52:1 female to male ratio (χ^2 = 3066.8, df = 1, p = < 0.001). Overall, size ranged from 41 cm to 550 cm TL with females of 201 – 230 cm TL caught in the greatest abundance, and females also dominating all larger length classes (Figure 5.2).

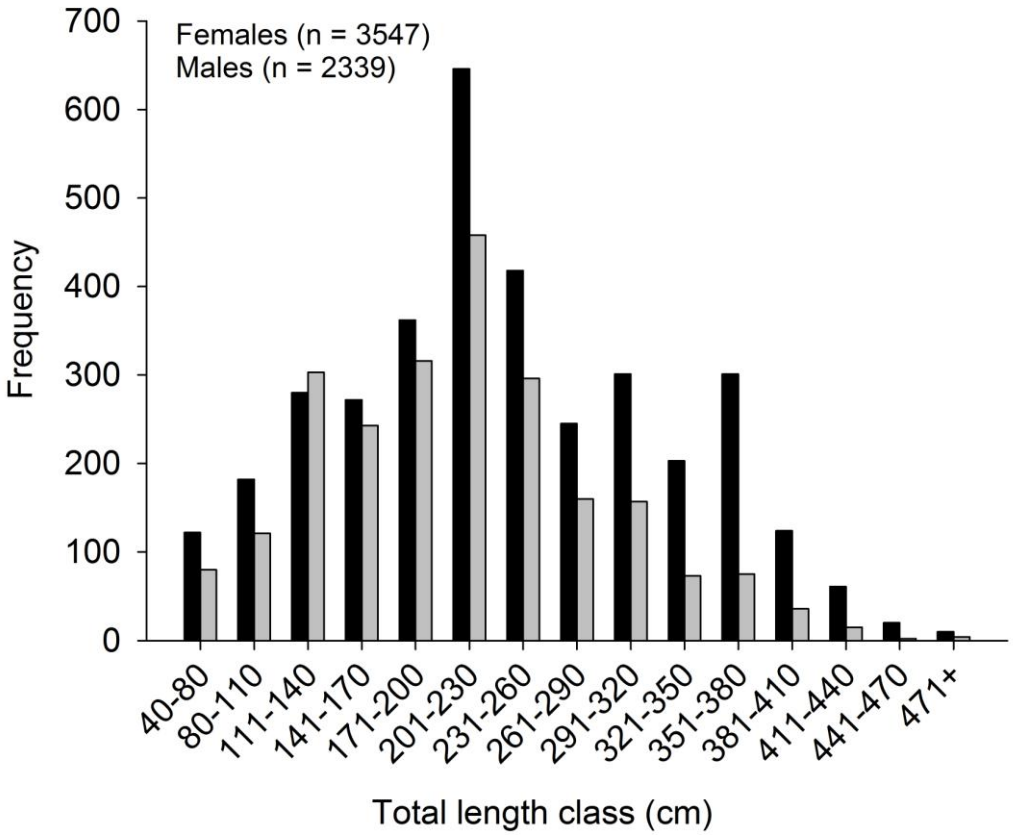

Figure 5.2: Length frequency distributions of female (black) and male (grey) *G. cuvier* samples used in this study.

From retained specimens, size-at-maturity was calculated from the clasper length measurements and calcification state from 45 males, and the ovary mass (g) and oviducal maximum width (mm) for females (n = 56 and 38, respectively). For males, a marked increase in clasper length was noted from 250 cm TL (Figure 5.3). The smallest mature male with fully calcified claspers was 276 cm TL, while the largest immature male with partially calcified claspers was 326 cm TL. Mean outer clasper length for maturing and mature males was > 20 cm and clasper growth appeared to asymptote at 23 – 25 cm once maturity is reached. Length at 50% maturity (L_{50}) for males was 297 cm TL. Sperm was present in all fresh clasper samples from mature males obtained during summer game fishing competitions.

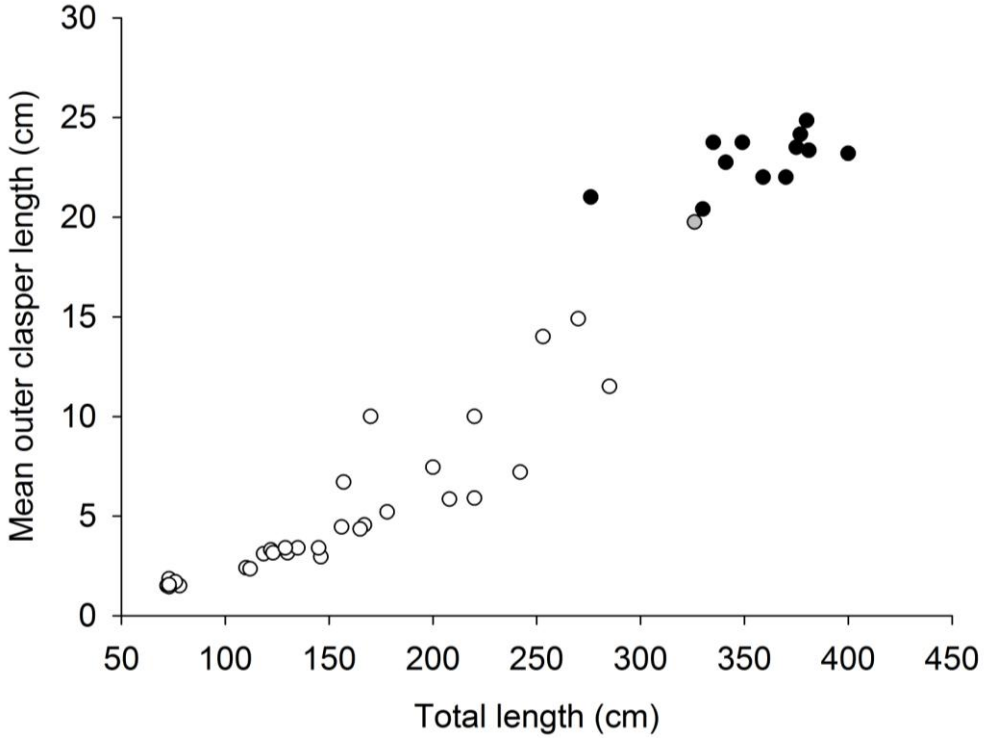

Figure 5.3: Relationship between mean outer clasper length (cm) and total length (cm) of male *G. cuvier* off the Australian east coast. White circles indicate immature sharks, grey circles indicate maturing sharks, and black circles indicate mature sharks.

The size of the oviducal gland provided the clearest separation between immature and mature females with a gland width of ≥ 60 mm present in all mature female sharks (Figure 5.4a). Ovary mass provided a reasonable indication of size-at-

maturity, even with some females in the oogenesis stage of the reproductive cycle phase (Figure 5.4b). Two females (299 cm and 308 cm TL) had developing oocytes, but the presence of small oviducal glands and suggested that they were not fully mature. Four females between 370 cm and 438 cm TL were undergoing vitellogenesis, with large, yolky oocytes in the ovary. Length at 50% maturity (L_{50}) was 325 cm TL. Length at 95% maturity (L_{95}) was only slightly higher at 326 cm TL. Maximum oocyte diameter (MOD) was 0.3 – 1.2 cm for immature females, and 1.0 – 2.7 cm for mature females, with the small MODs occurring during the non-reproductively active (resting phase) in mature individuals (Figure 5.4c). Similarly, the number of oocytes in each ovary in immature females was 9 – 49, and 38 – 189 in mature females (Figure 5.4d), with low numbers occurring during the resting phase in mature individuals.

5.4.2 Litter characteristics, gestation period and reproductive seasonality

Of the 3,390 female tiger sharks caught in the QSCP (1993 – 2014), 612 were over 325 cm TL (L_{50}), and 83 were reported to have been pregnant at the time of capture. Litter sizes ranging from 5 to 92 pups (26 ± 14, mean and SD), although small litters may have been an artifact due to pups being aborted due to capture stress, however a positive relationship was found between increasing litter size and maternal length (R^2 = 0.10, p < 0.005) (Figure 5.5). The sex ratio of the embryos was significantly biased towards females (1.26:1 female to male ratio; X^2 = 5.02, df = 1, p = < 0.001). Embryo lengths *in utero* were 10 – 86 cm TL and the smallest free-swimming neonates captured were > 60 cm – 90 cm TL. Internal yolk sac mass for 80 embryos (44 female, 36 male) from three different litters showed that yolk sac size generally decreased as pup size increased, however, there was considerable variation within each litter (Figure 5.6 and 5.7a). Shell membranes comprising spindle-shaped sacs enclosed in a thin casing of gelatinous membrane and containing a central yolk sac compartment were found in the posterior regions of both uteri in a pregnant 380 cm TL shark (Figure 5.7b).

Pregnant tiger sharks were captured all year round, although those with the largest pups (> 60 cm TL) were caught predominantly between November and January (Figure 5.8). Overlap in the capture of both early and late-term embryos in these months support a 15 – 16 month gestation period. Neonates (60 – 97 cm TL)

were captured predominantly in the first half of the year, indicating the summer/early autumn parturition of pups (Figure 5.8).

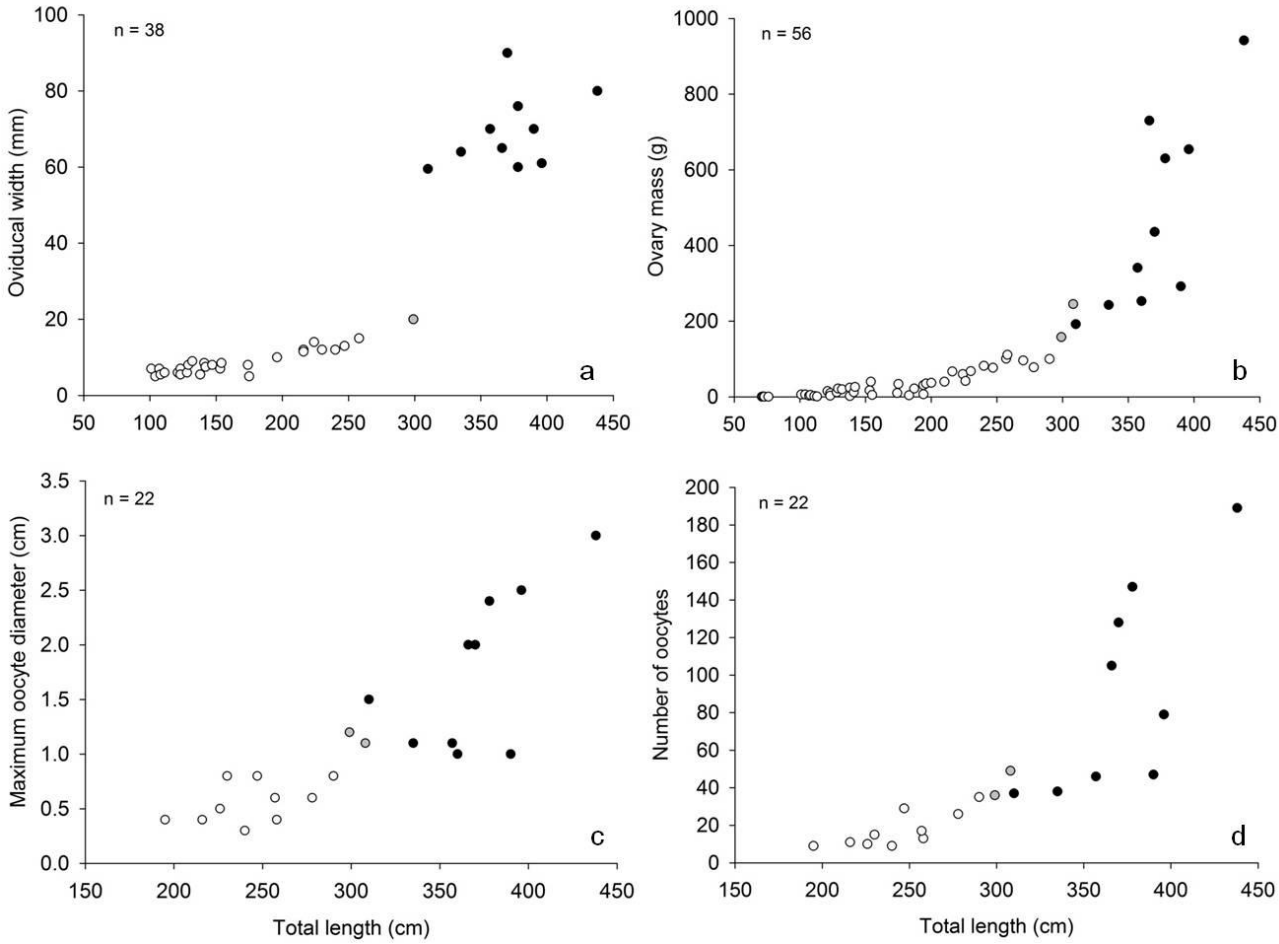

Figure 5.4: Female *G. cuvier* reproductive biology off the coast of Australia. Relationships between (a) mean oviducal gland width (mm) and total length (cm); (b) ovary mass (g) and total length (cm); (c) maximum oocyte diameter (cm) and total length (cm); and number of oocytes and total length (cm) (d). White circles indicate immature sharks, grey circles indicate maturing sharks, and black circles indicate mature sharks.

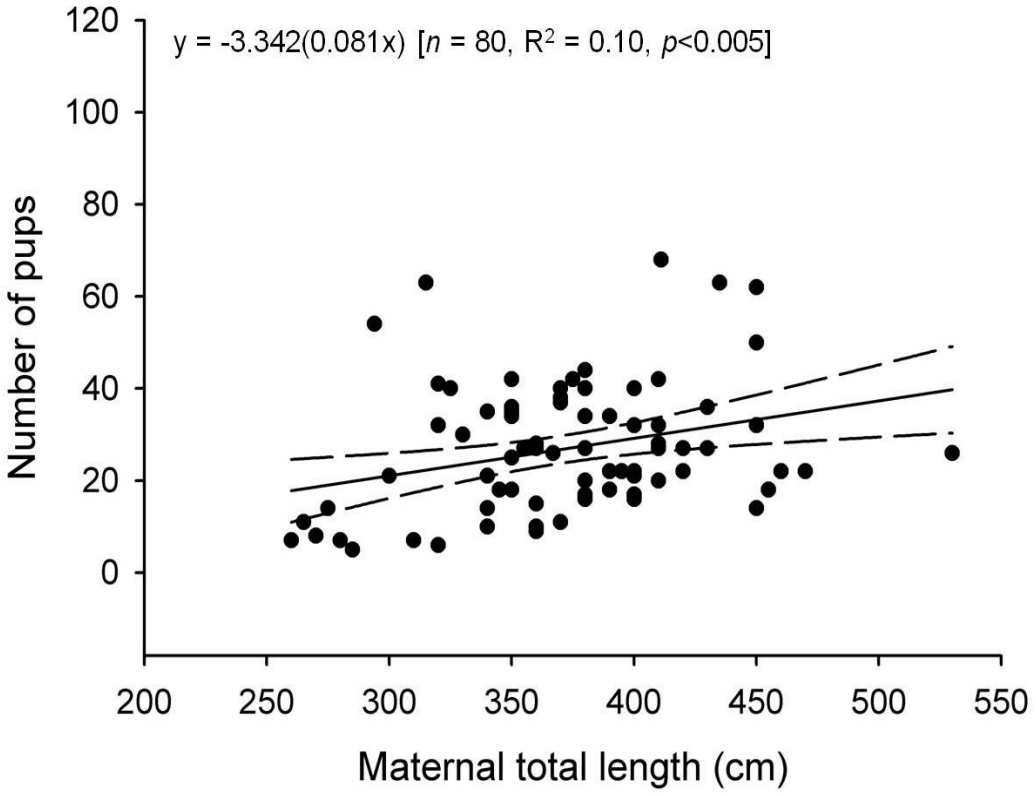

Figure 5.5: Relationship between embryo number and maternal total length (cm) of pregnant *G. cuvier* on the east coast of Australia. Plots are regression (–), with 95% confidence intervals (- - -) and raw data (●).

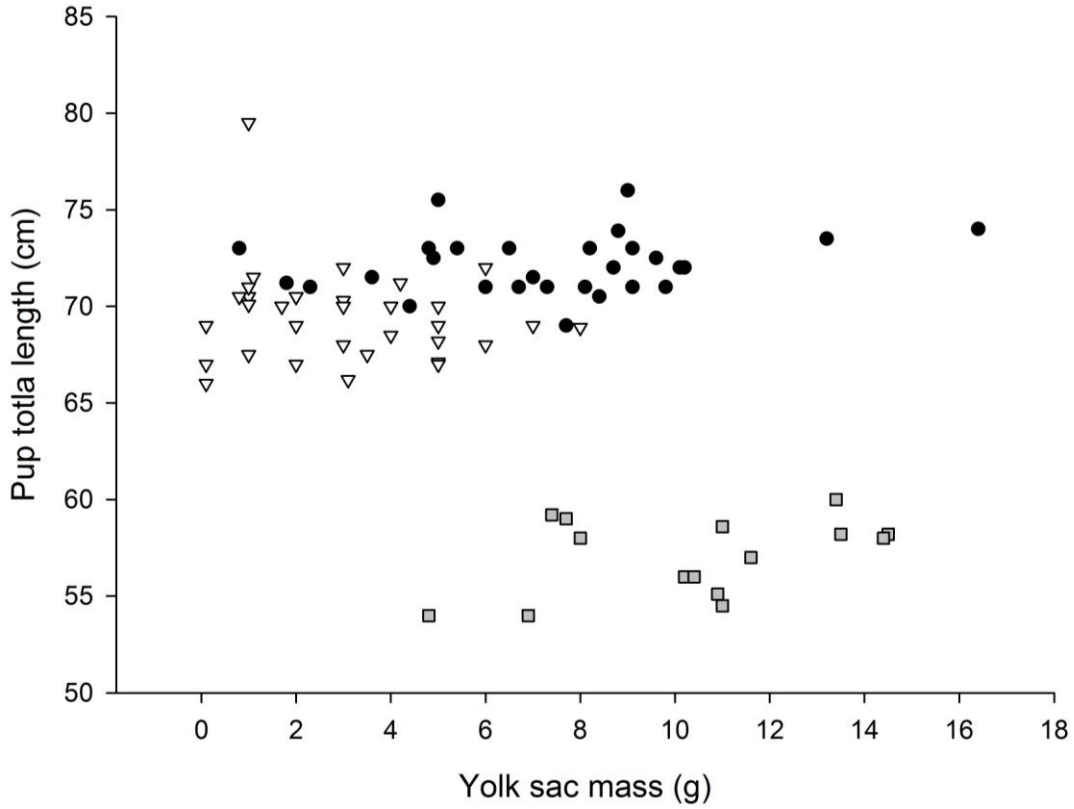

Figure 5.6: Relationship between pup total length (cm) and yolk sac mass (g) for in-utero pups from three *G. cuvier* litters on the east coast of Australia.

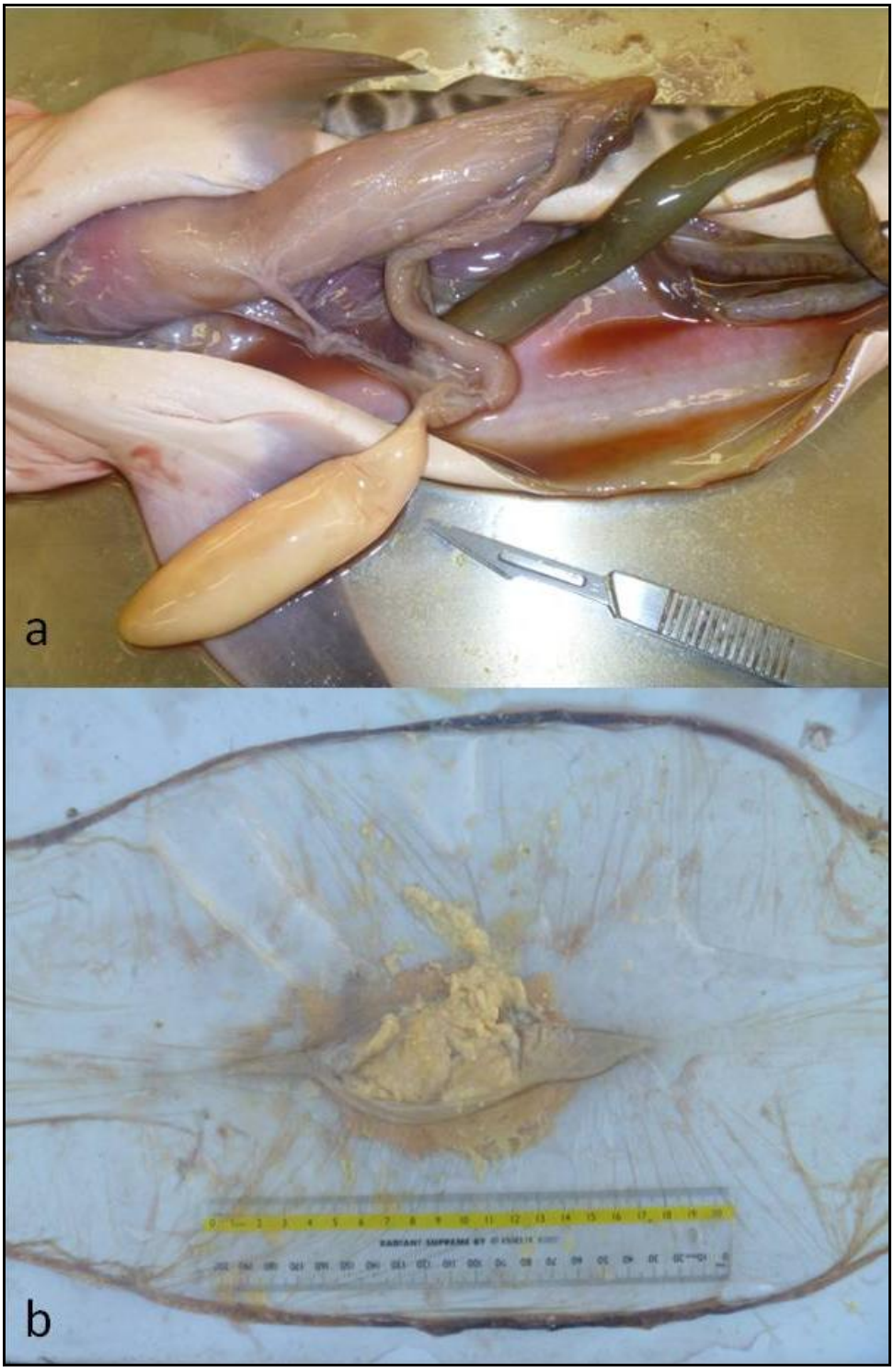

Figure 5.7: Pregnant 3.8m TL captured on the Gold Coast, Queensland, with (a) 73 cm TL pup containing large internal yolk sac (8.8 g), and (b) unfertilised yolk sac contained within gelatinous sheath.

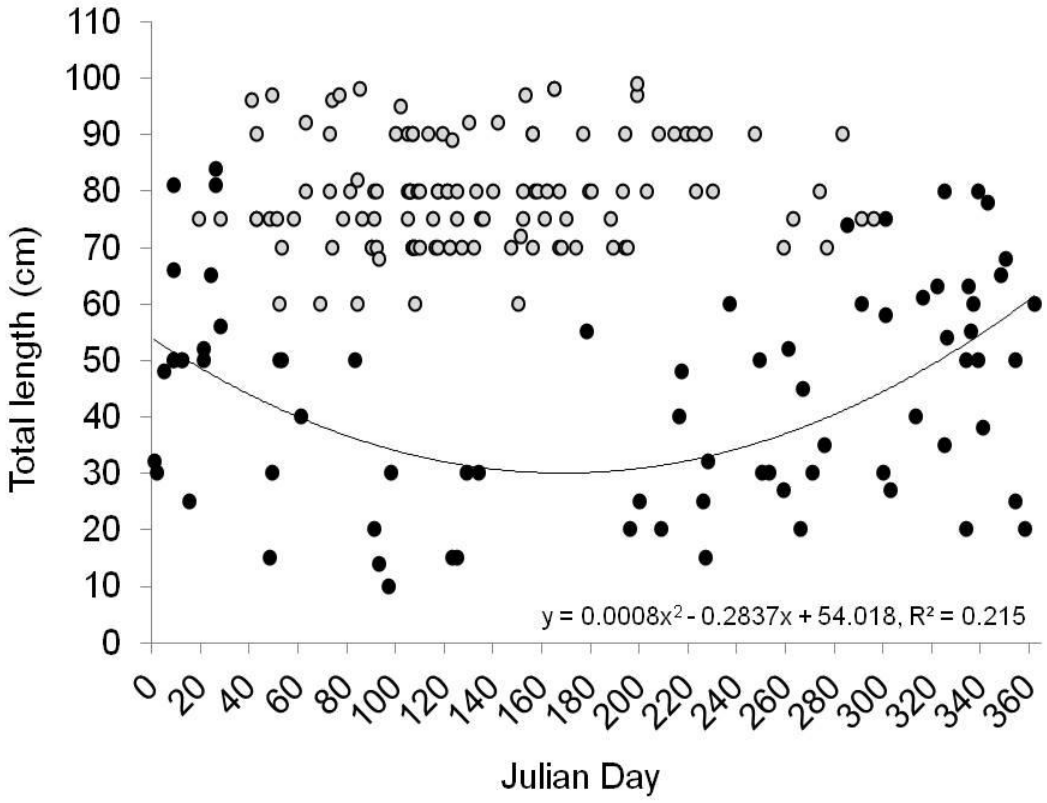

Figure 5.8: Relationship between mean total length (cm) of in-utero litters and total length (cm) of free-swimming neonates by Julian day for *G. cuvier* caught of the east coast of Australia. Plots are (●) in-utero pups, n = 76, and (●) free-swimming neonates, n = 121. Regression line indicates largest in-utero pups are captured during the summer months. Pup length data was not recorded for seven of the 83 litters reported in this study.

5.4.3 Reproductive cycle

Despite the relatively large sample size, the percentage of mature females that were pregnant particularly in the months December – January, were well below the number expected for a three year breeding cycle (Figure 5.9). Using an L_{50} of 325 cm TL for this population to determine the % pregnant resulted in about 30% of sharks being pregnant in the peak summer months. Changing the minimum size at maturity to 340 cm TL, previously used by Whitney and Crow (2007) in Hawaii to determine a triennial breeding cycle, did little to change the percentages (a 2% increase in December only) already achieved using the L_{50} calculated for this population.

Presumed recently deposited sperm was present in the posterior portion of the oviducal gland in a 357 cm TL female caught in December 2011. She had large vascularised uteri, consistent with recent pregnancy, and oocyte diameters were small (< 1.1 cm). Another female, caught in August (austral winter), also had small oocytes (< 1.1 cm), but oocyte diameters in three other females captured in February – March were large (> 2.4 cm). Sharks retained for multiple paternity analyses had litters of pups of 54 – 61 cm TL and 66 – 79.5 cm TL for sharks caught in August and December, respectively. Females were found in one of three reproductive conditions at any one time within a year as; a) gravid, b) first year non-gravid with small oocytes, and c) second year non-gravid with large oocytes undergoing vitellogenesis. These varying stages of reproduction point to a triennial breeding cycle for the east coast Australian tiger shark population (Figure 5.10).

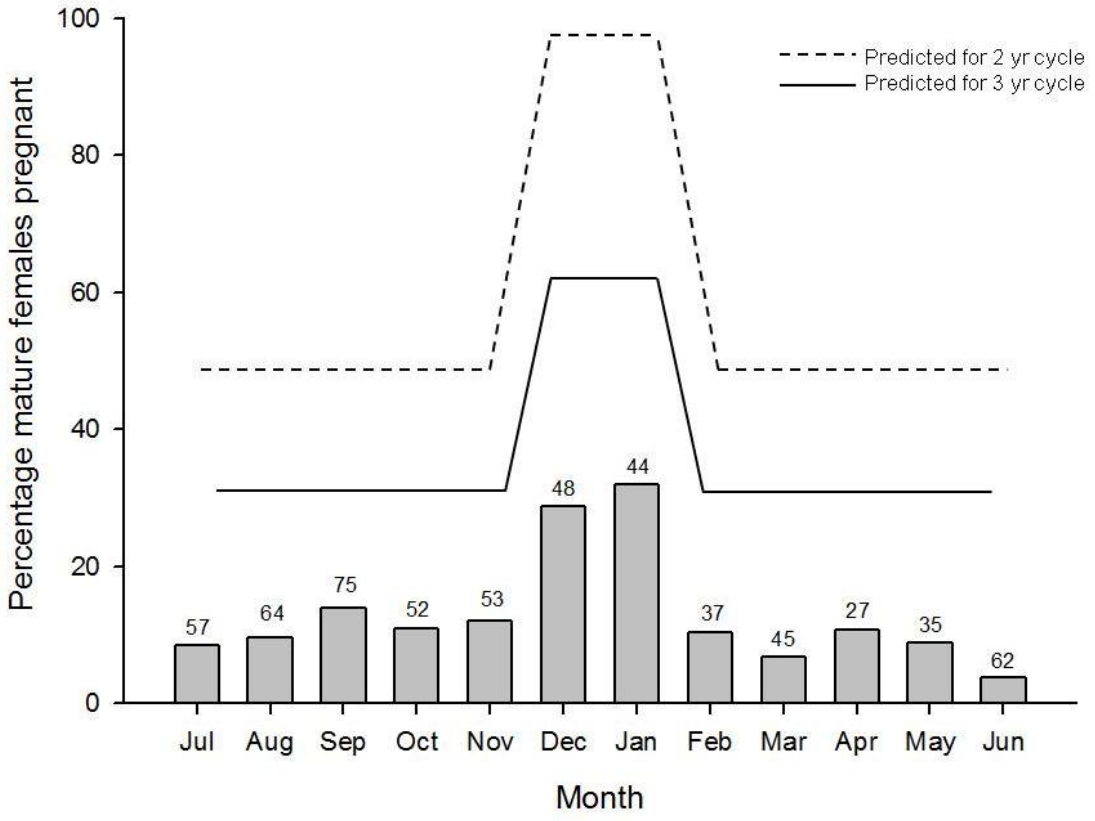

Figure 5.9: Percentage of mature female *G. cuvier* (> 325 cm TL, *n* = 599) that were pregnant for each month of the year off the Australian east coast (following Whitney and Crow, 2007). Numbers above bars indicate the number of mature females captured that month. Lines represent the percentage of females expected to be pregnant following a biennial reproductive cycle (- -), and a triennial cycle (–), assuming a 15–16 month gestation period.

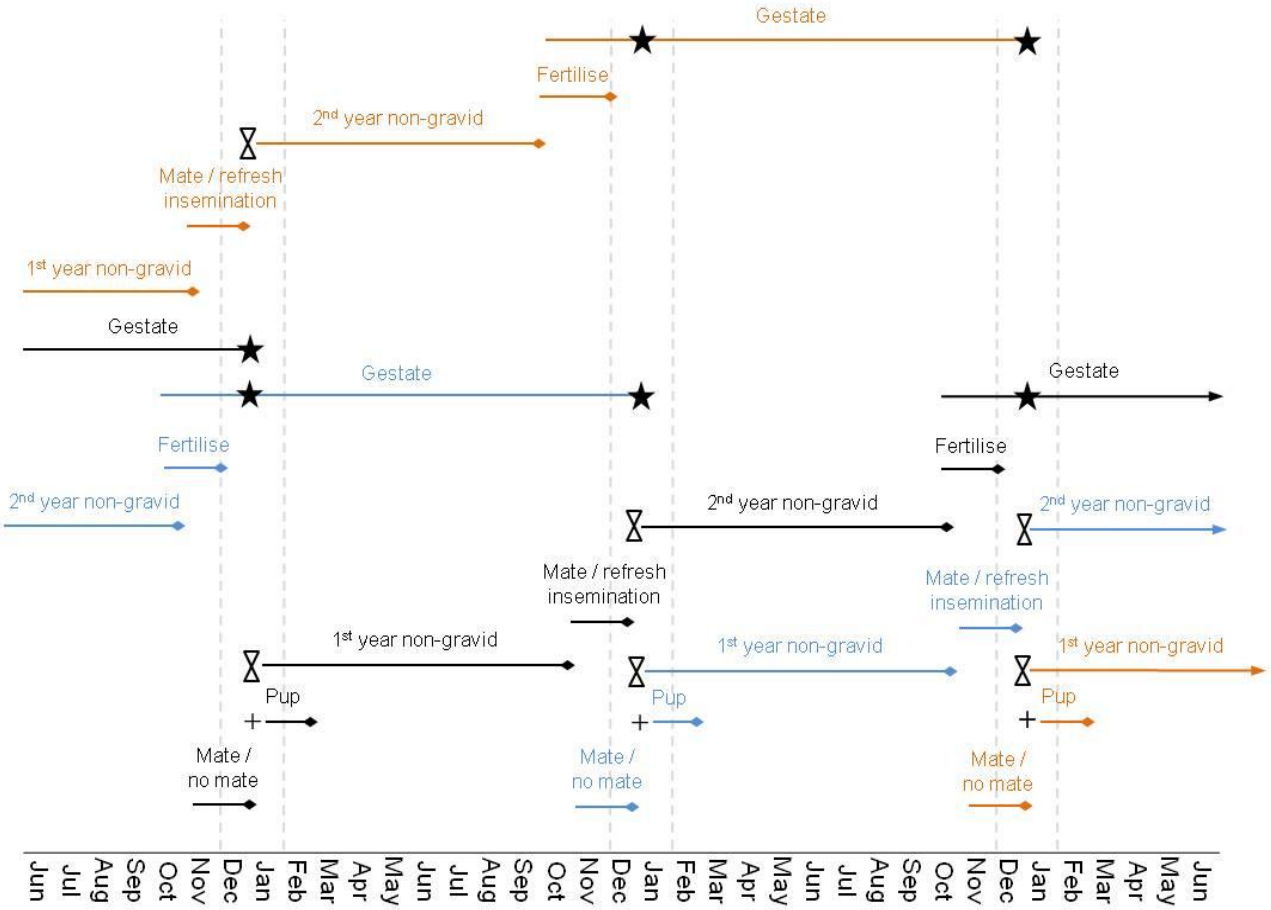

Figure 5.10: Proposed triennial breeding cycle for *G. cuvier* in the western Pacific region. During summer periods (- -), (★) indicates gravid females with small and large in-utero pups, (+) indicates females that have pupped, and (⧖) indicates either first (small oocytes) or second year (large oocytes) non-gravid females. Gestation is probably 15 –16 months. Sperm storage may be > 12 months and repeat insemination in subsequent years may occur.

5.4.4 Multiple paternity

Preliminary screening of adult genotypes from selected east coast Australian locations detected no disequilibrium (data not shown), and all locus pairs were in linkage equilibrium following sequential Bonferroni correction ($p < 0.05$). Mendelian inheritance of alleles at these loci was further supported by the complete concordance of mother offspring genotypes (112 comparisons). The nine loci had an average of 10.3 alleles (range 3 – 22) and unbiased heterozygosity of 0.72 (range 0.45 – 0.93). This allowed differentiation of siblings with high confidence (PIDsib = 0.0003).

Manual allele counting indicated that only one father contributed to each litter. None of the three litters where maternity was known had more than two paternal alleles for at least two loci. For the litter where the mother was not known, the total allele count per locus in the litter did not exceed 4, which implied a single sire. If two fathers contributed equally to litters, or with only moderate skew (66:33%), PrDM simulations indicated we had strong power to detect multiple paternity, even for the smallest litter size ($n = 16$, $p > 0.999$). However, detecting multiple paternity at high skew was more difficult (92.5: 7.5%; e.g. approximately 1 offspring out of 13 with a second father). The smallest litter size had a probability of 0.71 of detecting high skew, but for the largest litter this increased to 0.939, indicating that in all but the most extremely skewed scenarios, evidence of multiple paternity would have been detected.

The manual allele counting method to estimate the number of fathers was confirmed using the software Colony. Three litters were identified by Colony as being fathered by a single male. In the fourth litter, a single pup, out of a litter of 34, was assigned to a second father with high confidence (probability of substructure = 0.999). The second male assignment was based on two loci – however the pup was homozygous at these loci with an allele that matched its mother. Thus, while it is possible that this pup was the result of a second male gaining paternity, this assignment could also be due to allelic drop out. Only seven of the nine loci were amplified for this pup, and repeat genotyping was unsuccessful.

5.5 DISCUSSION

This study constitutes the most comprehensive analysis of the tiger shark reproductive biology of a single region to date. Successful mating in sharks with wide-ranging coastal and pelagic movements may depend on the rate of encounter between potential mates, particularly for semi-solitary species (Daly-Engel et al., 2006). This may be further compounded when the stock is impacted by fishing exploitation, decreasing the rate of encounter due to declines in abundance or changes in sex ratios of mature individuals (Daly-Engel et al., 2006). The capacity to rebound from population reductions is often directly linked to the reproductive potential of a species, therefore understanding a species' reproductive strategies are vital for effective fisheries management and conservation.

The length-frequency distributions of both male and female tiger sharks captured in this study were unimodal. Female tiger sharks dominated the larger size categories, which is consistent with previous Australian studies (Stevens and McLoughlin, 1991; Simpfendorfer, 1992a; Krogh, 1994; Simpfendorfer et al., 2001), and those conducted in the eastern United States of America (Branstetter et al., 1987; Natanson et al., 1999), but differs from observations in Hawaii where both male and female tiger sharks > 350 cm TL were regularly caught (Whitney and Crow, 2007). Size-at-maturity for male tiger sharks was generally attained at an outer clasper length of > 20 cm. The L_{50} for male sharks (297 cm TL) was consistent with the estimated size-at-maturity ranges reported by most studies elsewhere (> 290 cm TL (Clarke and von Schmidt, 1965); ~ 305 cm TL (Stevens, 1984b); ~ 310 cm TL (Branstetter et al. 1987); ~ 305 cm TL (Rivera-López 1970); ~ 292 cm TL (Whitney and Crow 2007)). Smaller lengths of male size-at-maturity have been reported in Brazil (237 cm TL; Alves, 1977), further indicating that regional differences in maturation are likely to occur. With the exception of Clark and von Schmidt (1965) and Branstetter (1987) who also measured male siphon sac development, all studies determined male sexual maturity from the size and/or calcification state of the claspers.

Female size-at-maturity was determined from measurement of several internal reproductive organ structures. Although both the number of oocytes and MODs generally increased with increasing shark length, there was some overlap between the number and size of the oocytes in the ovary between immature and mature sharks. This indicates that female tiger sharks do not reproduce annually and carry small eggs

during their resting phase (Whitney and Crow, 2007). Oviducal gland width provided the clearest indication of sexual maturity, with considerable gland enlargement occurring in sharks between 295 cm and 305 cm TL, with all females in this study fully mature at 326 cm TL. All females over this size had gland widths of > 60 mm, which was in contrast to Hawaiian tiger sharks where several large females > 325 cm TL still had oviducal gland widths of < 40 mm (Whitney and Crow, 2007), consistent with the observation that female tiger sharks in Hawaii mature at slightly larger sizes (> 340cm TL; Whitney and Crow, 2007) than those off the east coast of Australia.

Neonates (< 90 cm TL) and pregnant sharks were caught in all Queensland shark control locations, with the exception of Gladstone which recorded neither, indicating that nursery or pupping grounds are widespread. Gladstone is the only location in the QSCP that is truly estuarine, suggesting that females may not pup in these more sheltered, potentially brackish waters. Litter sizes were highly variable, but considerably smaller on average (26 pups per litter) compared to the ~ 32 pups per litter reported in other studies with reasonable sample sizes (Simpfendorfer, 1992a; Whitney and Crow, 2007). However, as litter size was found to positively correlate with maternal size, the smaller mean may simply reflect the size distribution of pregnant sharks in this study.

Previously, size-at-birth on the Australian east coast was estimated to be approximately 80 – 90 cm TL, based on data from the Townsville region (Simpfendorfer, 1992a). However, these estimates were derived from 1964 – 1986 QSCP data at a relatively small spatial scale, and smallest free-living individual caught was 84 cm TL. Since then, two smaller individuals were caught in 2001 and 2004, at 72 cm TL and 64 cm TL, respectively. In total, there have been 121 free-swimming ‘neonate’ tiger sharks caught within the QSCP since 1993, ranging from 60 cm TL to 99 cm TL. The largest recorded embryo was 86 cm TL in a 410 cm TL female caught off Bundaberg in 2000. The overlap in size ranges of free-swimming and embryonic sharks suggests that there may be several factors that determine the timing of parturition. Early estimates of size-at-birth were in the range of 51 – 76 cm TL (Compagno, 1984; Randall, 1992). Schwartz (1994) in the eastern US, and Whitney and Crow (2007) in Hawaii reported values of 76 – 89 cm TL, similar to those of Simpfendorfer (1992a). Small free-swimming tiger sharks of 46 – 51 cm TL reported in early records from the Gulf of Mexico (Baughman and Springer, 1950) and the north Atlantic (Bigelow and Schroeder, 1948) were considered to represent

premature births (Clarke and von Schmidt 1965). Observations of these small free-swimming tiger sharks are a likely result of females aborting pups due to capture stress; a behaviour observed and recorded by contractors working with tiger sharks in the QSCP. Pup abortion is a post-capture stress response that has been reported previously in several other elasmobranch species (see Branstetter et al., 1987; Rincon, 2007, Joung et al., 2008), and may also explain the low mean litter size and the few extremely small free-swimming neonates observed in this study. Further, the range of sizes in a given litter may be considerable, with pups ranging from 66 – 79.5 cm TL in one of the late-term litters analysed in this study. Assuming that complete parturition of all pups occurs at the same time, the natural size-at-birth for the east Australian population probably ranges from 70 to 90 cm TL.

Pregnant tiger sharks were captured all year round, although those with the largest pups (> 60 cm TL) were caught predominantly between November and January, suggesting pupping off the coast of Australia occurs in the austral summer months. Interestingly, no free-swimming neonates (< 99 cm TL) have ever been captured during November or December indicating that the pups born the previous summer likely grow larger than this in their first year of life. The capture of females carrying both early- and late-term embryos in the period from November to January also suggests that gestation in *G. cuvier* is longer than one year in the Pacific Ocean. Although Castro (2009) proposed a 12 month gestation cycle for Atlantic tiger sharks, Whitney and Crow's (2007) estimation of a 15 – 16 month gestation period for Pacific tiger sharks would explain the overlap in females at different stages of pregnancy during the summer months. Perhaps the 3 – 4 month gap in these estimates is merely a range between early and late season fertilisation, or that slight regional differences do exist between Atlantic and Pacific tiger shark populations.

Mating may occur before full-term pups have been birthed (Branstetter et al., 1987; Randall, 1992), which is supported by the presence of sperm at the posterior entrance of the oviducal gland in a 357 cm TL female that had very recently pupped in this study. Oviducal sperm storage in elasmobranchs has been well documented (Pratt, 1993; Hamlett et al., 1998; Parsons et al., 2008; Moura et al., 2011), however the strategy of sperm storage employed by different species varies greatly. Prasad (1945) was the first to identify oviducal spermatozoa in the posterior shell-secreting tubules in female *G. cuvier* from India. More recently, Pratt (1993) identified *G. cuvier* oviducal sperm through a smear preparation, surmising that the small amount

was consistent with long-term tubule storage. Given the semi-solitary nature of tiger sharks, the optimal time for copulation may not be compatible with the optimal time for fertilisation or birth (Moura et al., 2011). Reports of mating before parturition (Branstetter et al., 1987; Randall, 1992) and post-partum females with the presence of sperm in the uteri (this study) are in contrast with other studies that found post-partum females without the presence of sperm (Prasad, 1945). Given the apparent spatial coexistence of males and females of this species, females may opportunistically mate before they are ready for their next pregnancies.

Although a large number of pregnant sharks were assessed in this study, the high percentage (> 60%) of summer pregnancies reported in Hawaii by Whitney and Crow (2007), which justified their conclusion of a triennial breeding cycle for this species, was not found. This may be an artifact of the majority of the data on pregnant females being collected by independent shark control operators, which due to sea conditions may not have checked the pregnancy status of all mature females. It is likely that this also accounted for the small percentage (17%) of mature females pregnant reported by Simpfendorfer (1992a), using QSCP data from Townsville. Nevertheless, a significantly higher proportion of gravid to non-gravid females would have been reported if tiger sharks undertook a biennial reproductive cycle, as almost all females would have been pregnant during the months of December – January. The biological data obtained from this study supports a triennial cycle based on the presence of two females with large oocytes (> 2.4 cm) and high oocyte counts in February – April (indicating that they would be ripe for fertilisation in October – November), and the presence of another female with few, small oocytes (1.1 cm) in August, indicating a resting phase. The four pregnant females dissected in this study were all carrying well–developed embryos in August, October and December. Observation of these three phases fit entirely within the proposed cycles outlined in Figure 10, which indicates that between the summer periods of each year only a third of sharks would be pregnant. A similar reproductive strategy was also described in the school shark (*Galeorhinus galeus*), which justified a triennial breeding cycle for that species (Peres and Vooren, 1991). Despite biennial cycles being a common reproductive strategy for carcharhinids, a triennial cycle has also been proposed for dusky sharks (*C. obscurus*) based on a 22 month gestation period and a one year resting phase (Musick et al., 1993). Interestingly, as proposed for tiger sharks, the sperm storage in *C. obscurus* is consistent with long-term storage deep in the oviducal tubules (Pratt, 1993). Based on

the proposed triennial reproductive strategy, and the presence of females with and without oviducal sperm post-partum, opportunistic mating appears to occur during the pupping summer, and/or again the following summer, to potentially maintain the viability of sperm stored > 12 months. This raises the possibility that oocytes from single or repeated ovulations are fertilised by multiple males (Byrne and Avise, 2012).

Despite having 112 pups from four different litters, evidence for multiple paternity (> 2 paternal alleles, more than one offspring assigned to a second male) in tiger sharks from this population was absent. Instead, the data provided support for single-sired litters in tiger sharks. If multiple paternity does occur in tiger sharks, it does so at extremely low frequencies within litters (1/34; in 1 of 4 litters). Although multiple paternity is widely accepted as a common reproductive strategy in carcharhinids, the frequency and prevalence may vary between species, populations and even between conspecific individuals (Daly-Engel et al., 2006). Although only four litters were analysed in this study, several other studies analysing between 1 – 4 litters discovered multiple paternity in a range of sharks, including species that also employ an aplacental reproductive strategy (e.g. *C. altimus*, *n* = 1, Daly-Engel et al., 2006; *Hexanchus griseus*, *n* = 1, Larson et al., 2011; *Ginglymostoma cirratum*, *n* = 3, Heist et al., 2011; *Isurus oxyrinchus*, *n* = 4, Gubili et al., 2012; *C. carcharias*, *n* = 1, Gubili et al., 2012). Further, the large number of individuals tested for paternity in this study when compared with other studies of smaller litter sizes (see Byrne and Avise, 2012 for review), should have increased the chance of discovering multiple paternity across a litter, even at low frequencies. The presence of a single pup with two homozygous loci that potentially had a different sire was inconclusive, based on only 7 of the 9 microsatellite loci amplifying, and the repeat genotyping failed to validate the original results due to degraded DNA. Therefore it could not be confirmed that multiple paternity occurs in this species. With some studies suggesting that multiple paternity may maintain genetic variation in a population, or increase effective population size (Sugg and Chesser, 1994; Hoekert et al., 2002), there is a greater likelihood that some of the offspring in a litter will be more adaptive to changing environmental conditions (Yasui, 1998; Byrne and Avise, 2012). This might be particularly relevant in elasmobranchs, which generally exhibit a slower rate of molecular evolution than other vertebrates (Byrne and Avise, 2012). Compared with sharks that employ multiple paternity as a mating strategy, *G. cuvier* may be more susceptible to declines in genetic diversity as the number of potential mates decreases

with population size. Greater knowledge of the storage location and longevity of oviducal sperm in *G. cuvier* would also facilitate a greater understanding of the breeding processes in this oceanodromous species.

Understanding the reproductive strategies of commercially- and recreationally-exploited elasmobranchs is fundamental to implementing appropriate fisheries management regimes. Here we provide additional evidence that Pacific Ocean *G. cuvier* populations likely employ a triennial breeding cycle with a 15 – 16 month gestation period, as first proposed by Whitney and Crow (2007) in Hawaii. The lack of evidence supporting multiple paternity in this species may also influence the genetic diversity for this population. With most females not sexually mature until approximately 325 cm TL (~12 years of age; Holmes et al., In press), coupled with a triennial breeding cycle decreasing annual fecundity to around 33%, tiger sharks in this region may have a reduced capacity to withstand significant amounts of fishing pressure. Together with the recent catch rate declines identified on the Australian east coast (Holmes et al., 2012), additional management measures to ensure the sustainability of tiger sharks in this region may be required.

5.6 Acknowledgements

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Chapter 6: General Discussion

6.1 SIGNIFICANT FINDINGS OF THIS RESEARCH

The impacts of fishing activities on the abundance of large shark species are diverse, and the scale of commercial, recreational, artisanal and illegal fishing practices differ greatly among oceanic regions. Although the implementation of marine protected areas (MPAs) has been successful in reducing shark population declines in some areas (Dulvy, 2006; Bond et al., 2012; da Silva et al., 2013), these areas seldom encompass the full home range of larger shark species (Knip et al., 2012). The western Pacific region comprises of the east coast of Australia, New Zealand and an array of South Pacific Islands. Throughout this region, there is a complex of exclusive economic zones (EEZ) and territorial sea and archipelago waters interspersed with international high seas. The different management and monitoring regimes of neighbouring jurisdictions, coupled with a lack of fishing regulation in international waters, has resulted in increased threats to migratory shark species in this region (Dulvy et al., 2008).

Until recently, there were few empirical data to provide an indication of the population trends of *Galeocerdo cuvier* in the western Pacific Ocean. While the species was previously considered able to absorb moderate levels of fishing pressure in Australian waters (Simpfendorfer, 1992a), other studies in the Atlantic Ocean have documented significant local declines in tiger shark abundances (Baum et al., 2003). More recent estimates of the relative sustainability of different shark species in QLD revealed that tiger sharks rank as one of the highest in relation to the relative risk posed by commercial fishing operations (Gribble et al., 2005). Given their broad distribution, it is logistically and financially difficult to monitor tiger shark populations at various locations throughout their range. Further, long-term catch and catch rate trends are difficult to obtain, particularly as tiger sharks are generally considered a bycatch species in east coast Australian fisheries (Williams, 2002), and historical commercial logbook information has provided poor species-level reporting and inaccurate effort information. For this reason, the use of long-term shark control program information for deriving catch rate trends is advantageous. Often these data have been collected over prolonged temporal scales using standardised fishing methods, providing a critical fishery-independent monitoring tool when other information is lacking (Dudley and Simpfendorfer, 2006).

The use of historical Queensland Shark Control Program (QSCP) data in this thesis provided the first species-specific catch and catch rate analyses for tiger sharks over a broad spatial scale (Chapter 2). The significant decline in catch rates identified throughout most regions in QLD in this study, coupled with the ongoing declines observed in the NSW shark meshing program (Reid et al., 2011), indicate that the current level of catch of tiger sharks in this region may be unsustainable. However, the significant inter-annual variation in CPUE observed across the QLD coast indicated that a better understanding of the intrinsic and/or extrinsic factors influencing shark movements was needed to determine if catch rates are an appropriate proxy for population abundance of this migratory species. To better understand the potential exposure to fishery impacts across the western Pacific, identification of the migratory patterns and environmental factors that determine habitat use by tiger sharks was realised through the deployment of satellite tags (Chapter 3).

Acting at multiple scales, animal migration may influence population structure, govern ecosystem dynamics and influence evolutionary processes and patterns of local and global biodiversity (Nathan et al., 2008). Improving our knowledge of migration is therefore critical to many applied issues such as species conservation, ecosystem management and stock management of fisheries species (Chapman et al., 2012). In this study, some satellite tracked tiger sharks were found to move great distances, while others exhibited more localised movements. These movements were consistent with partial migration; where within a migratory population only some individuals migrate in a given season (migrants), while the rest remain in the same location (residents) (Chapman et al., 2011). Identification of the use of seasonally warm, prey-rich waters of NSW in summer, coupled with a contraction to sub-tropical QLD waters in the winter, indicated that water temperature plays an important role in the distribution of this species, at least at the southern extent of their range. Similar extrinsic influences on the movements of blacktip shark (*C. limbatus*) and spinner shark (*C. brevipinna*) populations have been identified as drivers for the seasonal migrations between higher and lower latitudes in the Atlantic Ocean (Castro, 1996; Ebert and Stehmann, 2013). Despite the majority of time spent in waters > 21°C, vertical dive profiles indicated that tiger shark visits to deep water habitat > 900 metres at temperatures as low as 5.9°C were common, although these visits were often brief and understanding the purpose of such dives requires additional research.

The extensive use of continental shelf waters with infrequent visits to nearshore environments in this study was unexpected, and it may be that tiger sharks are only occasionally exposed to inshore fisheries in Australia. Nevertheless, as a migratory species that was tracked moving across the broader southwest Pacific, the fishery impacts on this population also extend to the unregulated fishing in Coral Sea international waters, and artisanal fishing of the South Pacific Islands. Further, the impacts that long-term extraction of tiger sharks from the QSCP and NSWSMP since the 1960s has had on the virgin biomass of this population may be substantial, particularly as shark control programs are considered 'effective' because they remove large shark species from the water (Springer and Gilbert, 1963).

Catch rates that are analysed in conjunction with appropriate biological characteristics of a species provide a better understanding of population trends (Maunder et al., 2006). Further, adequate understanding of life history parameters is crucial to determine the extent to which a species' population would be affected by different fisheries operating within their range, and their ability to recover should stocks become depleted (Branstetter, 1990; Smith et al., 1998). This study was the first to provide a detailed analysis on the age, growth (Chapter 4) and reproduction (Chapter 5) of tiger sharks in the western Pacific region. Overall this population was characterised by slower growth rates than have been reported in other regions of the world. However, the presence of larger, older sharks in the age and growth analyses of this study may have had some effect on the resultant von Bertalanffy growth function (VBGF) parameters. Model effects such as higher L_∞ and k values derived from mark-recapture VBGF parameters may be attributed to the absence of older recaptured sharks in the sample, therefore comparison of growth rates at length may be more appropriate (Skomal and Natanson, 2003). Such variations in growth parameters between studies are not uncommon in large shark age and growth research, with differences in maximum age estimates reported between populations of white sharks (*C. carcharias*) in the western north Atlantic (Natanson, 2002), southern Africa (Wintner and Cliff, 1999), and the western North Pacific (Tanaka et al., 2011). A comparison of the VBGF growth curves for the same population of Gulf of Mexico bull sharks (*C. leucas*) even yielded considerable differences between subsequent studies (see Thorson and Lacy, 1982; Branstetter and Stiles, 1987).

Novel findings in this study include the presence of opaque centrum banding in pre-natal tiger shark litters consistent with in-utero development during the winter

months, and the occurrence of split and narrow banding in the tiger shark centrum that could potentially result in age underestimation in this species. Age underestimation in elasmobranchs is a component of growth research now receiving greater attention, with improving band-count and bomb radio-carbon assay technologies identifying even medium-sized elasmobranchs as potentially much older than first thought (Ardizzone et al., 2006; Francis et al., 2007), which has implications for local stock assessment and fishery management regimes. While variation in growth among conspecifics within the same region appears typical for tiger sharks, further assessment of growth rates for the Australian east coast population would benefit from a long-term study utilising vertebral calcein marking to validate band deposition, and a formal mark-recapture tagging program conducted by researchers and trained citizen scientists during recreational shark fishing activities. A greater understanding of the cartilage mineralisation processes associated with shark growth are also needed, particularly when the majority of shark age and growth studies rely on periodic annuli deposition to set the 'criteria' relating to band-pair counts to determine shark age.

The diversity of reproductive modes among the elasmobranchii, and the number of occasions that adaptations have arisen through evolutionary time, indicates that the elasmobranch reproductive system is highly adaptable, and that novel reproductive specialisations may still await discovery in this taxon (Waltrick et al., 2012). Indeed, the lack of evidence supporting multiple paternity in western Pacific tiger sharks was surprising given the wide-ranging movements and semi-solitary lifestyle of this species. Multiple paternity appears to be a feature of 25 to 100% of litters examined in other elasmobranch species, so its absence in the four litters examined here suggests that it is not a feature of the reproductive strategy of *G. cuvier*. Despite *G. cuvier* having the ability to produce large litters, the results in this thesis demonstrate that variation in size-at-birth within the same litter may be considerable (70 – 90 cm TL), with smaller sharks potentially having a higher rate of juvenile mortality (Morgan and Burgess, 2007). During the extensive analyses of the reproductive biological data it became apparent that the western Pacific tiger shark population likely employs a triennial breeding cycle, such as that proposed by Whitney and Crow (2007) for a population in Hawaiian waters. While their study justified a triennial cycle by the percentage of mature females pregnant each summer, the identification of females in three distinctive reproductive phases throughout the year in this study gave strong support for this proposed cycle. A triennial cycle, coupled with the potential for

single-siring of litters, indicates that *G. cuvier* populations are less likely to be resilient to even moderate levels of fishing pressure, as previously suggested by Simpfendorfer (1992a) and Dudley and Simpfendorfer (2006). Further, the identification of potential size- and sex-based segregation of male tiger sharks in this study may mean that males and females are differentially exploited, with more females being extracted based on the greater duration of their exposure to inshore fisheries and bather protection programs.

6.2 Future Directions

In addition to the aforementioned research that could be conducted to further the biological work on this population, novel research using genetic techniques to determine population structure, phylogeography and effective population size is needed to better understand how the extraction of tiger sharks by commercial, recreational and shark control activities over the past 100 years on the Australian east coast has affected their population status. Loss of microsatellite diversity may be an indication of overexploitation (Hauser et al., 2002), and an analysis of historical and contemporary gene structure from this population may highlight loss of allelic diversity due to fishing pressure, or even identify adaptations to a changing environment. Understanding genetic diversity, population connectivity and the trends in abundance (gleaned only from historical catch rate data to date), is crucial to the development of conservation goals for this near-threatened species.

Further work on *G. cuvier* movement ecology to determine how scale-dependent behaviours are shaped by, or drive, predator-prey interactions is essential to understanding the dynamics of neighbouring ecosystems and the connectivity among them. Although recent studies have begun to provide insights into the scale-dependent movements of sharks (e.g. Sims et al., 2011; Papastamatiou et al., 2013), there remain important gaps in our understanding of the movement drivers for species that are facultative 'partial' migrators. Due to a lack of empirical data, we are still unable to predict the transient and resident movement behaviour of tiger sharks, with more data needed on a larger number of animals across the full size range of both sexes. Analyses should occur in both the warm temperate/sub-tropics and tropics to gain a better understanding of how environmental conditions and changes in prey diversity

and abundance might also influence the transient/resident movement dynamic. This research would also facilitate our understanding of the top-down effects that tiger sharks are having on our coastal ecosystems (Heithaus et al., 2008).

6.3 SUMMARY

This thesis has provided a comprehensive overview of tiger shark fisheries, biology, and ecology in the western Pacific region. The catch, catch rate and shark size data from the shark control program suggests that significant declines, particularly in southeast Queensland, have occurred over a substantial period of time. The movement ecology of tiger sharks off the Australian east coast appears to be driven largely by water temperature, with individual sharks exhibiting a range of movement behaviours incorporating highly directional transient swimming, coupled with restricted swimming patterns repeatedly covering the same areas. Considerable use of the continental shelf habitat, coupled with the partially migrating fraction of the population in a given year, may explain some of the inter-annual variation observed in *G. cuvier* catch rates in nearshore waters. The age and reproductive data indicates that tiger sharks reach older ages, and grow at slightly slower rates, at least for the western Pacific population. Coupled with a triennial breeding cycle, variable size at birth and a semi-solitary lifestyle, *G. cuvier* may be more susceptible to overexploitation than previously thought. It is anticipated that the outcomes of this research will provide both fisheries managers and environmental policy makers with a sound understanding of the current fisheries catch rate trends of tiger sharks, as well as local empirical biological and ecological data that will provide a stronger basis for the sustainable management of *Galeocerdo cuvier* into the future.

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